JUL 30 '28

Vol. 20, No. 2 July, 1928

Medical Lib.

PARASITOLOGY

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CHICAGO: THE UNIVERSITY OF CHICAGO PRESS
(AGENT FOR THE UNITED STATES)

BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.

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[*Issued* 13 *July* 1928]

PRINTED IN GREAT BRITAIN

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VOLUME XX JULY, 1928 No. 2

A CONTRIBUTION TO THE STUDY OF THE DIPTEROUS PARASITES OF THE EUROPEAN EARWIG (*FORFICULA AURICULARIA* L.).

BY W. R. THOMPSON, PH.D., D.SC.

(*United States Bureau of Entomology.*)

(With Plates IV—IX and 4 Text-figures.)

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I. INTRODUCTION.

THE European earwig (*Forficula auricularia* L.) accidentally introduced some years ago into the United States, is now abundant in several of the Western and at least one of the Eastern States; it has become established also in New Zealand, where, according to Tillyard, it has become a major pest, eating into peaches, nectarines, and apricots and rendering them useless for sale.

As to the actual damage caused by earwigs, opinion seems to be divided. Some authors apparently consider that this insect is in the main carnivorous.

However this may be, it is certainly a creature very distasteful to many persons. In order to combat it, the introduction of the principal parasitic enemies of the earwig in Europe is being attempted by Dr Tillyard in New Zealand and by the municipal authorities of Portland, Oregon, in co-operation with the U.S. Bureau of Entomology.

The following paper, which has been prepared in the hope of facilitating the work of introduction, deals with the two Dipterous parasites of *Forficula auricularia* L. known to exist in Europe.

II. Review of the Literature.

The earliest mention of Dipterous parasites of earwigs appears to have been due to the Swedish naturalist C. H. Boheman, who stated in 1850 and 1851, that he had found an earwig with the abdomen unusually swollen and that on the day after the specimen had been pinned he found a Dipterous puparium protruding from between the thorax and the abdomen. From this puparium an individual of *Digonichaeta setipennis* Fall. emerged in May of the year following.

In 1853 G. Newport published a short paper on a Tachinid reared by him from earwigs collected in the vicinity of London. He described it as a new species under the name of *Metopia forficulae*, but this description is unrecognisable and as the type no longer exists it cannot be identified with certainty. It is doubtfully referred by Bezzi and Stein to the genus *Digonichaeta* (*Kat. Pal. Dipt.* **3**), but according to Nielsen (1912) this can scarcely be correct as the species observed by Newport was said by him to deposit its eggs upon the body of its host, which is not the habit of either of the known parasites of earwigs. It seems more probable, however, that Newport's account of the oviposition is simply mistaken and that the parasite he discovered was either *Digonichaeta* or *Rhacodineura*, as no others have been discovered in spite of the fairly extensive investigations subsequently made.

In 1863 Fr. Meinert in his *Anatomia Forficularum* mentions briefly having found on four occasions undetermined Dipterous larvae in *Forficula auricularia* L. and in *F. acanthopygia* Gené.

The next reference concerns *Rhacodineura antiqua* Meig., which was reared for the first time from the larvae of *Forficula tomis* Kol. by W. Rodzianko, who published in 1897 an account of his investigations in the *Horae Societatis Entomologicae Rossicae*, but as the paper is in Russian with only a brief *résumé* in German the author has not hitherto obtained due credit for his observations.

In 1909 there appeared Pantel's admirable and comprehensive "Recherches sur les Diptères à larves entomobies" which contains many interesting observations on both *Digonichaeta setipennis* and *Rhacodineura antiqua*, cited by Pantel as *Ceromasia rufipes* Mg. as the specimens had been misdetermined by the specialist to whom they were submitted. In 1912, in the second instalment of his "Recherches sur les Diptères à larves entomobies," the same author

described in detail the effect exerted by the larva of *Digonichaeta* on the reproductive system of the earwig; in 1914 he published a careful study of the circulatory system of *Rhacodineura* (under the name of *Ceromasia rufipes* Mg.) and finally in 1916 gave a succinct account of the anatomy and biology of this species in a short note published in the *Bulletin de la Société Entomologique de France.*

In the meantime, J. C. Nielsen, the Danish student of the Tachinidae, described in parts II and IV of his "Undersogelser over entoparasitiske Muscidelarver," some of the principal anatomical and biological characteristics of *Digonichaeta* and *Rhacodineura.* Some further data were added by the present writer in three papers published in 1915, 1920 and 1924, the first on *Digonichaeta,* the second and third on *Rhacodineura* and other Tachinids of the same ecological group. Finally, in 1924, there appeared a short notice by A. M. Altson, which is of interest in that it records for the first time actual observations on the reproductive habits of the parasites. The author also mentions some hyperparasitic enemies of the Tachinids.

The following study of the Dipterous parasites of the earwigs comprises an original account of the anatomy and biology of the two species, together with a brief summary of what is known in regard to their biology.

III. *DIGONICHAETA SETIPENNIS* Fall.

Larva, Stage I (Pl. IV, fig. 5).

The first-stage larva of this species was described by Nielsen in 1912 and by the author of this paper in 1915. The description given by Nielsen, based only on the study of a cast skin, is in part erroneous; that given by the author of this paper was incomplete. A new and detailed description has therefore been prepared.

Dimensions: L. 0·619 mm., w. (larva somewhat flattened by the cover slip) 0·190 mm. The newly hatched larvae are rather elongate and slender resembling in form those of certain Dexiids.

The cuticular armature of the larva is striking and characteristic. With the exception of the head and the last segment of the body which are transparent and colourless, bearing only a few feebly chitinised elements, the segments are dark brown in colour owing to the presence of strongly pigmented plates, bands and spines, the only naked areas with the exception of the conjunctivae, being small median ventral patches on some of the anterior segments.

The elements composing the cuticular armature are of several types. On the anterior margins of the segments there exist on the dorsal surface flattened spines, directed posteriorly and whose bases are 3–4 times as long as broad. The posterior margins bear dorsally small, dark nodules, those of the anterior rows punctiform, those near the posterior margin having the form of short dashes running longitudinally, the cuticle between these elements being slightly but distinctly pigmented. The space between the anterior and posterior

elements of the dorsal region is occupied by a large oblong heavily pigmented plate which occupies on the abdominal segments somewhat more than the anterior half of the dorsum. The pleural regions of the body bear narrow elongate dark brown chitinous ridges. Towards the borders of the ventral regions these become shorter and are slightly prolonged posteriorly so as to form spines with short acute points and elongate bases. On the ventral surface the spines are short and acute, of a more ordinary type.

Head bare dorsally and laterally presenting only a few slender very feeble spines on the ventral surface behind the buccal opening. Segment I bearing dorsally on the anterior two-thirds 4 rows of flat spines of which the anterior are small and acute, the posterior large and plate-like, roughly polygonal in outline, on the posterior third a crescent-shaped dark brown plate, incompletely interrupted medially, bearing on either side of the mid-dorsal line a very distinct transparent spot containing a sensorial organ, ventral surface with several rows of rather small dark brown nodules, pleural regions with flattened rounded plates. Segment II with a rather narrow roughly oblong plate, about 4 times as wide (from side to side) as long (postero-anteriorly) situated in the middle of the dorsal area; behind this plate are 6 or 7 rows of minute nodules, in front of it 3 or 4 rows of rather broad flattened scales, the anterior ones small and acute, the posterior elements, which are partly fused with the anterior margin of the dorsal plate, roughly polygonal, plate-like. Pleural region with about 3 rows of dark brown ridge-like scales, very slightly pointed posteriorly. Ventro-lateral regions with somewhat similar but shorter and more strongly pointed elements, the median ventral area, which is about twice as long as wide, with small dark punctiform nodules. Segment III is much like II, but the dorsal plate is a little shorter and wider, being about 6 times as wide as its length. The scales in front of it are longer and broader than on the preceding segment. The pleural and ventral regions are similar to those of segment II. On the fourth segment the dorsal plate is about as broad as on segment III, but longer in its median third which extends almost to the anterior margin of the segment, being separated therefrom only by a row of small acutely pointed scales. The lateral parts of the plates are narrower and provided on the anterior border with notches into which fit the points of the scales lying in front of the plate. Behind the plate are 4 or 5 rows of small chitinous nodules, of which each occupies the centre of a pale brownish area, the separation between these areas being however in general indistinct. The pleural regions bear numerous elongate ridge-like scales as on the preceding segments. On the ventral surface the spines are shorter and more acute, except on the posterior margin where they are feeble and reduced to fine short chitinised lines, and in the middle of the ventral area where there is a roughly fusiform area which is laterally and posteriorly naked, but bears in the middle of its anterior region 8 or 9 rows of minute nodules. On segment V, the dorsal plate is only very slightly broader than on the preceding segment, but is of uniform length. Its anterior border, which is dentate and bears scales difficult to dis-

tinguish from the surrounding chitinous plate, is separated from the anterior border of the segment by a row of moderately elongate acute spines. Between the posterior margin of the plate and the posterior border of the segment are 5 or 6 rows of nodules like those described on the preceding segment. As on the preceding segments, the pleural regions bear elongate rib-like spines, those on the anterior two-thirds being strong, elongate and darkly coloured, those on the posterior third short pale and thread-like. Just behind the middle of the ventral surface is a small, oblong, spineless area, in front of which are 5 or 6 rows of minute nodules and which is prolonged laterally on each side into a rather indistinct narrow band of spineless cuticula extending to the edge of the pleural region. The rest of the ventral region bears numerous spines, those towards the mid-ventral region being short and small, those towards the ventro-lateral regions larger and more elongate. On segments VI–X, inclusive, the form and arrangement of the plates and spines differs little from that described for segment V. The anterior margin of the dorsal plate on these segments is, however, somewhat nearer the anterior margin and fuses with the anterior row of spines, its anterior border being dentate. On segments IX and X the lateral diameter of the plates decreases like the diameter of the segments themselves. The pleural regions resemble those of the preceding segments. The ventral region on segments VI–X also differs little from that of segment V, but the spineless median transverse band is narrower and the elements immediately anterior to it larger than on the anterior segments. The last segment of the body differs greatly from the others. It is transparent and under a low magnification it appears to be spineless. The dorsal surface bears scattered nodules, minute and almost colourless, the pleural regions bear anteriorly several rows of pale brown rib-like spines arranged in a group of a more or less triangular form, with its apex directed posteriorly. The ventral surface bears a median triangular patch of similar but paler rib-like spines, the base of this patch extending almost to the posterior margin of the segment, the apex almost to the anterior margin.

In this stage the larva is metapneustic. The posterior spiracles (Pl. V, fig. 12) open on the posterior border of the dorsal surface. Each felt chamber terminates in a pair of respiratory papillae situated in a distinctly convex brownish protuberance, bearing several pale transparent spots, the openings of the peristigmatic glands. The felt chambers are pale in colour, slender and elongate, about 15–20 times as long as wide (l. 0·0576 mm., w. 0·0028 mm.).

The sensorial organs (Pl. IV, fig. 6; Pl. V, figs. 12, 13) are well developed though difficult to locate among the darkly pigmented spines and plates. The pseudo-cephalon bears ventrally the usual group of maxillary sensoria and dorsally two pairs of remarkable sense organs. Those of the anterior pair, which exist in various Dexiid larvae, are outwardly directed, short club-shaped organs, about 0·0054 mm. in length, each composed of an enlarged distal portion which is colourless and a narrow neck-like base, which is distinctly pigmented. Each of these clavate sensoria is situated on a rather indistinct

circular area. Just behind these organs on the dorsal surface are situated the antennae which are of very unusual form, having no counterparts among Tachinid larvae with the exception of a few species of the Melanophora group parasitic in woodlice (Thompson, 1917). Each antennary organ consists of a cylindrical elongate basal portion, pale brown in colour, measuring about 6 times as long as its diameter (l. 0·0108 mm., w. 0·0018 mm.) tapering rather abruptly to a point and terminating in a long thread-like distal portion, at least 4 times as long as the basal part. Each antennary organ is situated on a circular area about 0·0072 mm. in diameter, bounded posteriorly by a narrow dark brown marginal band of the form shown in the figure.

The sensorial organs on the body segments are of two sorts: setae and small circular sensoria. As the larva of *Digonichaeta setipennis* is not likely to be confused with any others, it is not necessary to describe the arrangement of these organs in detail. On the thoracic segments the dorsal region bears a number of circular organs. The pleural regions bear circular organs and two setae, one situated dorsally, the other ventrally. On segments II and III the ventral seta is much longer than the dorsal. On each of these segments the ventral region bears circular organs and Keilin's organ[1], which consists in these species of a pair of very distinct setae, one about twice as long as the other. The arrangement of the setae on the abdominal segments differs from that on the thorax. The pleural region bears dorsally on each side a short fine seta, and ventrally a group of three, placed close together along a horizontal line a little distance behind the middle of the segment. The two outer setae are short and slender, the inner one stout, rather strongly pigmented and elongate, extending posteriorly to a point some distance beyond the posterior margin of the segment. On either side of the ventral surface near the posterior border of the segment there exists a very characteristic short, stout, dark brown sensorial organ whose form is that of a truncated cone.

The last segment of the body bears sensoria in the form of slender elongate setae, of which there are 5 pairs, one dorsal, two lateral and two ventral. The appended figures show the arrangement of the more important of these sensoria.

The buccopharyngeal armature (Pl. V, figs. 8, 9) differs in form from those of all other Tachinid larvae known to me (l. about 0·096 mm.; of the anterior tooth seen from above, about 0·018 mm.; of the intermediate region to the anterior end of the space between the dorsal wings of the basal region, about 0·6 mm.; of the dorsal wings, about 0·085 mm.). As in the majority of first-stage Tachinid larvae it is without articulations. It terminates anteriorly in a very slightly curved acute stylet whose base appears to be surrounded on the ventral side by a sheath-like projection from the anterior end of the intermediate region. This latter has the form of a straight elongate rod, quadrangular in section, whose width is about equal to its height and whose length is about

[1] Keilin's organ is a group of sensorial setae situated at the point where the pedicels of the histoblasts of the legs attach to the hypodermis.

8 times its width. Towards the beginning of the anterior third the intermediate region presents in its lower side a distinct but shallow notch shown in the figure (Pl. V, fig. 9). The canal of the salivary gland opens into the pharynx just in front of this point; towards the base of the intermediate region a pair of small translucent spots are visible. The basal region is very short and feebly developed in comparison with the rest of the armature and the distinction between the dorsal and ventral wings is not very apparent. The dorsal wings, which, like the intermediate and anterior regions are thick, heavily chitinised and black with excess of pigmentation, are rather markedly divergent and rather strongly enlarged posteriorly with the posterior margin truncate. Viewed from above each bears, attached to its posterior outer angle, a pale brown oval plate. The anterior lateral plates are irregular in form; each is united by a rather narrow pedicel to a heavily chitinised median nodule which lies dorso-anteriorly to the median tooth of the mouth armature.

Larva, Stage II.

Length varying in my material from about 1·5 to about 3·0 mm. Nielsen (1912, p. 239) describes the skin simply as studded with many fine scattered spines. As a matter of fact, the spines which are small and short but rather broad and fairly heavily pigmented are arranged in bands according to a very unusual and characteristic plan.

The head appears to be spineless. Segment I bears an anterior band comprising 2 or 3 rows of small, short spines posteriorly directed, and a posterior band comprising 3 rows of larger spines anteriorly directed. On the pleural region this band presents in the posterior side a semicircular notch comprising an area of spineless cuticula in which is situated the anterior stigma. The anterior margin of segment II is bare, except in the ventro-pleural region where there is a group of a dozen small spines, but the posterior border bears a broad band of about 5 rows of spines, anteriorly directed; this band is limited to the ventral and pleural regions, the dorsal aspect of the segment being practically spineless. On segment III, the anterior border is spineless, though there are a few elements in the middle of the pleural region, but on the posterior border there is a broad band of anteriorly directed spines including 4 or 5 rows of elements and limited to the lateral and ventral region, the dorsum bearing only a few spines on the posterior border; on segment IV there is a short pleural or pleuro-ventral band on the anterior border, composed of two irregular rows of small posteriorly directed spines; on the posterior border there is a broad band of anteriorly directed spines as on segment III, but extending further up around the sides of the segment towards the dorsum. On the following segments the disposition of the spines is in general similar to what has been described except that the posterior band, which is complete, becomes considerably broader in the pleural regions on the posterior segments. On segments VII–X inclusive, the ventro-pleural regions bear on the anterior borders numerous small scattered spines posteriorly directed, this group

fusing at its posterior margin with the anterior edge of the posterior band whose spines are, however, anteriorly directed; the last segment bears an anterior band comprising a dozen or more rows of rounded and only slightly pointed spines directed backwards; this band passes behind the anal opening in the middle of the ventral region, and is broadest on the pleurae.

In this stage the larva is anatomically amphipneustic; but the anterior spiracles (Pl. VIII, fig. 33) are very small and may have no respiratory function; the felt chamber is long and slender and terminates in from 3 to 5 rather ill-defined respiratory papillae (l. 0·06 mm., w. 0·004 mm.); the posterior felt chambers (Pl. IX, fig. 45) on the contrary are well developed, short and stout, about twice as long as wide (l. 0·06 mm. approx., w. 0·028 approx.); each felt chamber terminates in two straight elongate spiracular slits.

The sensorial organs are greatly reduced in size as compared with those of stage I, most of them being now practically invisible; the antenna (Pl. VIII, fig. 26) is now short and inconspicuous, consisting of a transparent hemispherical cupule mounted on a cylindrical base (l. 0·008 mm.); the "claviform" and maxillary organs are about as in the first stage; the body segments bear each at least two pairs of short small sensorial organs, cylindrical in form and heavily pigmented.

The buccopharyngeal armature (l. 0·240 mm.) (Pl. V, fig. 14; Pl. VI, figs. 18, 19) is absolutely different from that of stage I. No articulation exists between the various regions which are solidly fused together; considerable variation exists in the shape of the various regions; the anterior and intermediate regions, which are not differentiated one from the other, are united at the anterior extremity by a dorsal band forming part of the dorsal wall of the atrium; the lower anterior corner of the anterior region is slightly produced into a pair of short semi-oval rounded teeth, of which the lower is slightly larger than the upper; the sclerite of the salivary duct is fused laterally with the lower borders of the intermediate region, as is usually the case; in front of this sclerite there is an independent sclerite, very heavily chitinised, with a recurved anterior border to which muscles are attached and which is the result of a very heavy chitinisation of the ventral wall of the atrium; the anterior margin of the dorsal wing of the basal region of the armature is not distinctly differentiated, the cuticle separating it from the upper border of the intermediate region being here chitinised and pigmented; the posterior end of the dorsal wing sclerite is rounded; the interalar emargination is also rounded; the ventral wing of the basal region is somewhat longer than the dorsal wing.

Larva, Stage III.

In this stage, under low magnification, the skin of the larva appears to be spineless, and was so described by Nielsen. It bears, however, numerous colourless conical spines which are very minute and visible only under strong magnifications. The exact distribution of these spines is difficult to make out; they appear to be more abundant on the ventral side than on the dorsal where they

are distributed over practically the whole surface of at least the intermediate segments.

In this stage the larva is quite definitely amphipneustic. The anterior spiracles (Pl. IX, fig. 46) are inconspicuous, each lying in a minute but rather deep invagination in the skin, each being encased in a truncate conical evagination of the cuticle, light brown in colour; the felt chamber or atrium, which is rather short and stout, terminates in a variable number (5–8) of short rounded papillae (l. of felt chamber 0·06 mm., w. 0·036 mm. approx.). The posterior spiracles (Pl. IX, fig. 40) are very prominent; each consists of a heavily chitinised, black cylindrical evagination of the body wall, about 1½ times as long as its diameter (l. 0·36 mm., w. 0·24 mm. approx.) and bearing on its distal surface a number of stigmatic slits arranged as shown in the figure, very variable in length, form and number; as the figure shows, the stigmatiferous tubes are very closely approximated basally, being separated only by a very narrow strip of unchitinised cuticle.

The sensory organs are in this stage very inconspicuous and even more reduced than in stage II; the antennal organ, as in the former stage, consists of a slightly convex distal portion situated on a short cylindrical base.

The buccopharyngeal armature (Pl. VI, fig. 16) is rather variable in form (l. 0·16 mm. approx.). As in the second stage, no trace of an articulation exists between the various regions usually distinguished; the anterior regions, which are connected anteriorly by a narrow dorsal bridge of chitin, terminate irregularly; there are no definite mandibles; the hypopharyngeal plate (Pl. V, fig. 15), situated as in the second stage, is oval or semicircular in form; its anterior border is recurved, its surface presents on its inner side a well-marked reticulum whose posterior borders bear fine sharp spines directed forward and upward into the buccal cavity; towards its posterior border this sclerite bears on each side a pair of small circular sensory organs. The epipharyngeal plate (Pl. VIII, fig. 31), which is in the upper wall of the buccal cavity or atrium, is much smaller. It bears on each side one large and two small circular sensory organs. The sclerite of the salivary gland, uniting the inferior borders of the intermediate region, traverses the floor of the pharynx just behind the hypopharyngeal plate; the basal region is very well developed, the area between the anterior border of the dorsal wing and the dorsal border of the intermediate region being in this stage unchitinised; the ventral wing is much longer than the dorsal wing and presents near its base an irregular pale spot.

Puparium (Pl. IX, fig. 36).

L. about 50 mm., w. at middle about 30 mm. Dark red or red-brown, subshining, often somewhat flattened dorso-ventrally, rounded anteriorly, rather acute posteriorly; spiracles situated on the posterior end of the longitudinal axis, elongate, black, markedly divergent but almost touching at their bases, anal opening on the under side, its distance from base of the stigmatic tubercles

about equal to the length of the tubercles; anterior spiracles very inconspicuous.

The pupal respiratory apparatus (Pl. IV, fig. 7) of *Digonichaeta* is of the reduced type; the prothoracic cornicles are absent, only the internal spiracles exist. These bear about 100 respiratory papillae arranged along 5 or 6 radiating branches of the end of the atrium.

Internal Anatomy of the Larva.

In its internal anatomy, the larva of *Digonichaeta setipennis* does not differ very greatly from the larvae of such non-parasitic Muscids as the house-fly (Hewitt, 1914) *Miltogramma punctatum* (Thompson, 1921) or the apple maggot (Snodgrass, 1924) for as Keilin (1915) has pointed out, the larvae of the Cyclorhaph Diptera, in spite of an extraordinary diversity of habits, are remarkably uniform in structure.

The following condensed account of the internal anatomy refers, unless otherwise stated, to the adult larva.

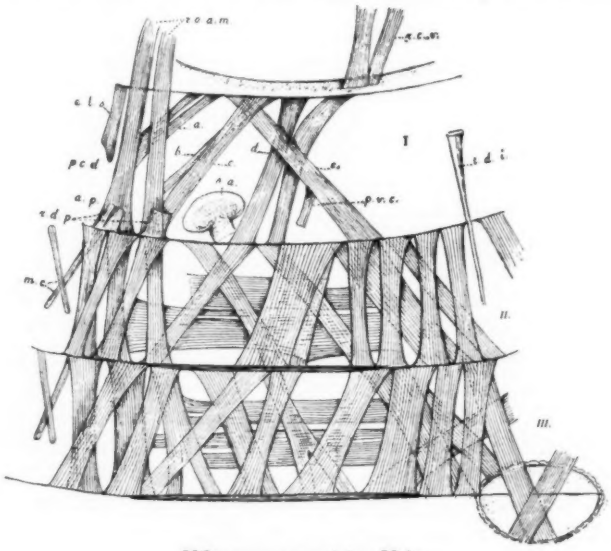
The body wall is composed, as in all insects, of a layer of cuticle, underlying which is the usual layer of hypodermal cells. The cuticle is delicate, being less than 1 μ in thickness. On account of its thinness the primary and secondary cuticular layers cannot be clearly distinguished. With Mann's methyl-blue eosine mixture the cuticle stains bright blue while the sensorial organs are rose coloured. The hypodermis consists of a single layer of pavement epithelium, the cells of which are much smaller and more numerous than in such larvae as *Miltogramma punctatum* or *Calliphora erythrocephala*, the average dimensions being here about 0·0126 mm. × 0·009 mm. as against 0·054 mm. × 0·048 mm. in *Miltogramma*. Furthermore, while the cells in *Miltogramma* and *Calliphora* are plano-convex, having the form of hanging drops, in *Digonichaeta* the inner surface of the hypodermis is perfectly flat. No definite topographical relation appears to exist between the hypodermal cells and the cuticular spines. The spines are situated sometimes opposite the nuclei but more frequently opposite the internuclear regions.

The muscular system of the larva is rather complicated. On account of lack of time and material it has not been possible to investigate it in detail. However, as the literature on the internal anatomy of the parasitic Muscids is as yet rather meagre, we have thought it worth while to compare the pharyngeal musculature and the tegumentary musculature of the abdominal segments with the homologous regions in the non-parasitic larva of *Miltogramma*, described in a previous paper, from which several figures are here reproduced (Text-fig. 1 and Pl. VII, figs. 22, 23, 24).

The results of this comparison are of considerable interest in view of the difference in habit between the larva of *Miltogramma*[1] and *Digonichaeta*. Although the former is non-parasitic, living as an inquiline within nests of

[1] The muscular system of *Sarcophaga falculata* Pand. is also practically the same as that of *Miltogramma*.

Halictus where it feeds upon the honey collected by the bee, while *Digonichaeta*, as we have seen, is an internal parasite of the earwig, the abdominal musculature of these two species is practically identical. The only differences which have been detected up to the present as far as the number and disposition of the fibres are concerned consist in the absence in *Digonichaeta* of two of the ventral oblique muscles, one of the pair 19–20 and one of the group 23–25 being absent in *Digonichaeta*. The muscle fibres are however much more delicate than in *Miltogramma* and *Sarcophaga*, the difference being especially in the area of the cross-section of the elements. The feeble development of the



Miltogramma punctatum Meig.

Text-fig. 1. Integumentary muscular system of first three thoracic segments, third-stage larva; left side seen from within. *a.–e.*, muscles of the first segment; *a.p.*, insertion of the pharyngeal depressor; *c.l.s.*, elevator of upper lip attached just in front of *p.c.d.*; *m.c.*, cruciate muscles; *p.c.d.*, insertion of dorsal cephalic protractor; *p.v.c.*, ventral cephalic protractor; *r.c.v.*, ventral cephalic retractors; *r.d.p.*, dorsal pharyngeal retractors; *r.o.a.m.*, retractors of the antennomaxillary complex; *t.d.i.*, stalks of the histoblasts of the first thoracic legs.

muscle fibres is of course correlated with the sedentary life of this internal parasite, whose movements are very restricted.

The musculature of the buccopharyngeal apparatus (Pl. VI, fig. 19) is also similar to that of *Miltogramma* (Pl. VII, figs. 23, 24). On each side of the posterior part of the buccopharyngeal mass are inserted, as in *Miltogramma*, two dorsal muscles and one ventral; of the dorsal muscles, the posterior pair—the *pharyngeal depressors*—attach in the mid-dorsal line, near the posterior border of the first thoracic segment, the anterior pair—the dorsal protractors—which in *Rhagoletis pomonella* are indistinguishable from the pharyngeal depressors, according to Snodgrass (1924), forming a single muscle, are attached

in the mid-dorsal line in front of the pharyngeal depressors. The ventral muscle, called by Hewitt the *ventral cephalic protractor* and by Snodgrass the *lateral protractor*, is attached to the body wall towards the middle of the ventro-lateral region, a little distance ventrad of the anterior spiracle. Just in front of the level of the imaginal disc of the labium, not far from the anterior end of the intermediate region is inserted a muscle which attaches on the line between segments I and II, a little lateral of the mid-dorsal line; this is the muscle termed by Hewitt the *stomal dilator*, but which I have termed the *dorsal pharyngeal retractor*, as its insertion appears to me to preclude the idea of the function indicated by the name given by Hewitt. In front of this muscle is another, inserted on the dorsal wall of the pharynx at a point just in front of the epipharyngeal sclerite and attaching on the body wall of the mid-dorsal region, just laterad of the dorsal protractors; this muscle which Hewitt wrongly believed to attach to the mandibular sclerite[1] of the house-fly larva, and called in consequence the "mandibular extensor" muscle, may be termed the *elevator of the labium*. In addition to these muscles there exist in the larvae of *Miltogramma* and *Sarcophaga* four additional pairs of important muscles of which two control the mandibular sclerites, one retracts the lower lip of the buccal atrium while the fourth opens the salivary duct. In spite of a careful examination the muscles of the salivary duct have not been discovered in *Digonichaeta*. The mandibular and labial muscles exist, but, as might be expected, in view of the peculiar conformation of the anterior front of the buccopharyngeal armature in *Digonichaeta*, they are somewhat modified. The *dorsal mandibular muscle* or *mandibular elevator* (termed by Snodgrass the *mandibular extensor* and described incorrectly by Hewitt as part of the so-called "*stomal dilator*" group), which attaches posteriorly to the side of the buccopharyngeal mass on a level with the ventral wing of the basal sclerite, is represented in *Digonichaeta* only by a fine fibre attached anteriorly to the pharyngeal epithelium near the anterior end of the lateral sclerites. The *depressors of the mandible* or *mandibular flexors* (Snodgrass, *l.c.*) are attached to the pharyngeal mass ventrad of the elevators but anteriorly they are inserted, together with the *labial retractors* from which they cannot really be distinguished, on the inner side of the recurved chitinised lower lip, which has been described in connection with the buccopharyngeal armature. In *Miltogramma*, as will be seen from our figure, the mandibular depressor attaches directly to a small accessory sclerite possibly homologous with Hewitt's so-called "*dentate-sclerite*" situated behind the base of the mandible; the insertion of the muscles in *Digonichaeta*, if homologous, thus indicates that the chitinised lower lip is a morphologically composite structure resulting from a fusion or uniform chitinisation of the dentate sclerites or mandibular apodemes and the lower lip.

[1] Hewitt describes the mandibular sclerite of the house-fly larva as a median unpaired sclerite, but as several authors have shown (see Keilin, 1917) it is in reality double as in other second- and third-stage Muscid larvae.

The *intrinsic musculature* of the buccopharyngeal organ consists mainly of an anterior set of dorso-ventral muscles attached dorsally to the inner side of the pharyngeal wings and ventrally to the dorso-pharyngeal wall, and a posterior set of transverse muscles attached to the sides of the dorso-pharyngeal wall. Intercalated between the transverse muscles are a few supplementary dorso-ventral muscles.

The *salivary glands* are of the usual type: they extend from about the level of the anterior border of segment II to about the posterior border of segment IV. The cells are large and project into the lumen of the gland. The cytoplasm is dense, deeply staining and slightly granular; the nucleus is large, of the type described by Pantel in his paper on *Thrixion* (1897), with a large eosinophile nucleolus and an elongate convoluted band of chromatine. Each gland opens into a duct lined with chitin and provided with annular thickenings, and fusing with that of the opposite side to form a median unpaired duct opening into the ventral wall of the pharyngeal cavity above the sclerite of the salivary gland (Pl. VI, fig. 17). The oesophagus (Pl. VI, fig. 21) is of the ordinary type and terminates a short distance behind the cerebroid ganglia in the usual piriform oesophageal valve.

The mid-intestine is much less elongate than in most Muscids, including perhaps the majority of the Tachinids, the deficiency in length being, however, compensated by an increase in the surface of the posterior part of the organ which extends in the adult larvae as a rather voluminous elongate sac through segments II–IX inclusive.

In the majority of non-parasitic Muscid larvae and in a good many Tachinids the anterior end of the mid-intestine is provided with one or two pairs of more or less elongate diverticula, the *gastric caeca*. In the *Digonichaeta* larva these organs do not exist.

The *mid-intestine* is lined with a single layer of epithelial cells and provided with a delicate external muscular layer. In the anterior slender portion of the organ the epithelial cells, while variable in form in various regions, are in general uniform in size, being all large cells with nuclei about 20μ in diameter. In the dilated portion, however, there are two types of cells: large cells (diam. about 60μ) with large nuclei (diam. about 28μ) and small cells (diam. often only 20μ or less) with small nuclei (diam. 12μ or less). The small cells in the intestine of a second-stage larva stained and mounted *in toto* are disposed in irregular rings around the large cells. When a section of the intestine is examined the arrangement of these elements can be made out more clearly. The small cells lie near the basal membrane, towards the periphery of the intestinal wall, overgrown, as it were, by the large elements which project into the lumen of the alimentary tract. The small cells are probably the "replacement cells" frequently described by students of Muscid metamorphosis and destined to form by their multiplication the adult intestinal epithelium. The large functional cells are filled with vacuoles, particularly on the side of the nucleus towards the intestinal lumen where the striated border is sometimes so distended as to

give the impression that it has burst and that the cell was fixed at the moment when its contents were pouring out into the cavity of the intestine. However, as the contents of the vacuoles have been dissolved by the clearing agent employed they evidently contained fat globules, so that the distended cells are actively absorbing food material. The contents of the alimentary canal, which do not appear to be surrounded by any peritrophic membrane, present vacuoles similar to those in the intestinal cells. Whether the mid-intestine of the larva secretes digestive enzymes in addition to its function of absorption, or whether such digestive ferments as are required are produced by the salivary glands alone, is at present uncertain and can only be determined by careful physiological studies. The cells in the dilated portion of the intestine are much flatter and more vacuolated than in the anterior region.

At its posterior extremity the mid-intestine suddenly diminishes in calibre, then broadens to form a short ampulla into which open the *Malpighian tubes*; just behind their insertion is the well-known "imaginal ring," composed of rapidly proliferating cells destined to form the adult hind-intestine and well developed even in the second-stage larva.

The *hind-intestine* does not differ especially from that of the non-parasitic Muscids. Its cells, which project into the lumen of the digestive tract, are lined with chitin. The circular muscle fibres which surround it are not as in *Calliphora* (Perez, *l.c.*) intracellular but are definitely external to the basal membrane. The intestine terminates in the ventral surface in the posterior border of segment X; its opening is surrounded by a plate of epithelial cells of the same nature as those of the hind-intestine itself. Similar structures, which exist in certain other Tachinid larvae, were considered by J. Pantel to have a respiratory function in parasites which live plunged in the body fluids of the host.

The relative lengths of the different regions of the intestinal tract in the *Digonichaeta* larva are as follows:

Oesophagus ...	0·476 mm.
Oesophageal valve	0·178 ,,
Mid-intestine ...	2·975 ,,
Stomach ...	1·428 ,,
Hind-intestine ...	1·309 ,,
Total	6·366 mm.

The *tracheal system* has been partly described in connection with the external anatomy of the larva and pupa and does not demand special consideration. It is mainly composed of a pair of lateral longitudinal trunks united in the second thoracic and last abdominal segment by two principal commissures in addition to intermediate secondary commissures. The tracheoles are of the usual type without thickenings or enlargements. The rudimentary spiracles, which are present on segments II–X inclusive, are situated as in the larvae of *Miltogramma* and *Sarcophaga*, in the anterior angle made by the

inter-segmental muscle 12, the recti-pleural muscle 10 and the oblique pleuro-ventral muscle 11 (Pl. VII, fig. 22). No lumen apparently exists in the tracheae connected with these spiracles, but the latter are visible in the larva as minute circular depressions which can only be detected when their exact situation is known.

The *fat body* consists of irregular sheets of cells extending between the integumental musculature and the internal organs, the most important part of the adipose tissue being a layer which is situated on each side of the body between the longitudinal tracheal trunk and the body wall. An interesting characteristic of the fat cells in *Digonichaeta* is that they are *binucleate*.

The *circulatory system* has not been studied in detail. It extends as in other Muscids from the posterior border of segment X to the buccopharyngeal mass and lies along the mid-dorsal line. It consists of four fairly well defined regions: (1) the posterior region or heart, extending from the posterior border of segment X into the posterior part of segment VIII, closed posteriorly and divided into chambers separately by well marked lateral valves bordered on each side by 7 or 8 large uninucleate pericardial cells and narrowing towards its anterior end where it passes into (2), an intermediate region whose diameter is much less than that of the "heart" and which is bordered with a large number of minute pericardial cells arranged in a narrow rather irregular band on each side of the vessel; (3) an anterior region without pericardial cells beginning a little in front of the level of the anterior end of the oesophageal valve and extending to a point between the posterior part of the cephalic imaginal discs, where it passes through the group of cells known as Weismann's ring, beyond which the ventral side of the vessel disappears; this part of the vessel (4), extending forward into the buccopharyngeal mass constituting the so-called "gutter."

Under the *excretory system* are usually included the *Malpighian tubes*, the *pericardial cells*, *Weismann's ring*, *ventral nephrocytes* and *oenocytes*.

The *Malpighian tubes* (Pl. VI, figs. 20, 21) are four in number arranged in two pairs, a posterior and an anterior. The posterior tubes, which are shorter than the anterior, are situated in segments IX–XI inclusive; the anterior tubes run forward on either side of the mid-dorsal line, to about the second abdominal segment, then bend abruptly and run backwards to about the fourth abdominal segment. The structure of the posterior tubes and of the ascending portion of the anterior tubes is not strikingly different from that of other Muscids except that as our figure (Pl. VI, fig. 21) shows they are shorter than usual.

The recurrent portion of the anterior tubes is however characteristic. In the majority of other Muscids which have been examined the recurrent region is dilated, extremely thin-walled, with cells lacking the striated border present in the other regions of the Malpighian tubes. This region is generally filled with carbonate granules[1] and specialised for the excretion of carbon dioxide.

[1] And not urates as stated by Roubaud in his paper on the hibernation of Muscids.

In *Digonichaeta* the structure of the recurrent branch is scarcely different from the rest, except for a very short and relatively thin-walled region at the extreme end of the tube comprising some 15–20 cells. Living specimens examined showed a white, finely granular substance, which is perhaps $CaCO_3$, in the basal part of the posterior tubes and in the ascending part of the anterior tubes; but the recurrent portions of the anterior tubes appeared to be empty.

The *pericardial cells* have been referred to in connection with the circulatory system. Weismann's ring surrounds the dorsal vessel at the level of the supra-oesophageal ganglia and consists of a ring of compact tissue composed of numerous cells with densely staining basophile cytoplasm and small, densely staining nuclei; it seems to be prolonged anteriorly above the blood vessel as a flat short plate: the *ventral nephrocytes*, though perhaps present, have not been detected in the material examined.

The *oenocytes* are arranged as in *Miltogramma* and the Tachinid larvae which have been studies, in 7 paired groups situated in segments IV–X inclusive, each group comprising several flattened cells, some of which are usually elongate, their long axis being parallel to the circumference of the body; they are situated between the muscles and the hypodermis in the space between the dorsal recti-muscles (3, 4) and the pleural recti-muscles (10) in front of the circular muscles (13) (Pl. VII, fig. 22). In *Miltogramma* and *Sarcophaga* these cells are mono-nucleate, but in *Digonichaeta* they are binucleate, like the cells of the adipose tissue, which is curious, as oenocytes are ectodermal and fat cells mesodermal in origin.

The nervous system (Pl. V, fig. 10; Pl. VI, figs. 19, 20, 21; Pl. VIII, fig. 26; Pl. IX, fig. 38) has not been specially studied. It presents, however, one unusual feature which deserves special mention. At the anterior extremity of the ventral nerve mass, one finds in the first-stage larva, more especially at the beginning of the first stage, a rounded lobe separated from the remainder of the ventral mass by a distinct constriction. The cerebroid ganglia, especially in the young larva, are slightly more elongate or less spherical than in most Tachinid larvae.

The *imaginal* discs (Pl. VI, figs. 19, 21) are practically identical in number and position with those of *Miltogramma* and *Sarcophaga*. The hypodermal discs, composed of cells destined to replace the hypodermis of the larva, comprise a small area on each segment around the opening of the rudimentary spiracle and two independent areas, one situated in the latero-sternal region underneath the most ventral member of the recti-muscles (12), the other situated just dorsal of the intersection of the oblique muscles 7 and 7 *a*. The discs of the head and mouth parts, wings, legs, abdominal appendages and tracheae are similar to those of *Miltogramma*.

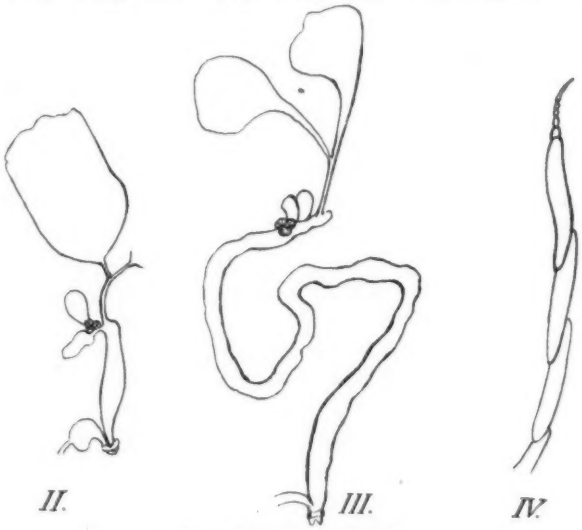
The genital organs are represented in the larva by a pair of rudiments, spherical in form, situated opposite the anterior margin of segment IX dorsad of the main tracheal trunk.

Cytology. The remarks regarding the cytology of the salivary glands (nuclei, chromatin, nucleolus) apply to the majority of the tissues of the larva.

The *Digonichaeta* larva in section appears almost empty as compared with the *Miltogramma* larva; the musculature is hardly visible, the integument is much more delicate; the intestine much less voluminous. On the whole, however, the difference between the free-living and parasitic larvae is surprisingly slight, considering the great differences in their mode of life.

Reproductive System of Adult Female.

In *Digonichaeta*, according to J. Pantel (1909), the young ovaries are massive, voluminous compared with the size of the fly, and rather elongate. They comprise about 40 ovarioles, developing at a very early age, in each of which there are to be found, two days after emergence, perhaps even at the time of emergence,



Digonichacta setipennis Fall.

Text-fig. 2. Reproductive system of immature adult female.
Text-fig. 3. Reproductive system of mature adult female.
Text-fig. 4. Ovariole of adult female. (All after Pantel.)

3 or 4 full-sized eggs, overlapping at their extremities as shown in the figure and a small number of very undeveloped ovarian chambers. The developed eggs apparently represent the total number deposited by the fly. They very soon begin to descend into the uterus even in the unfertilised female, but are not replaced in the ovarioles so that a uterus full of eggs is invariably accompanied by small and atrophied ovaries.

The paired oviducts are short. The unpaired oviduct, termed by Pantel the "anterior uterus," is rather long and slender. There are three spermathecae with somewhat piriform capsules and very short ducts. The accessory glands are very short and stout, a little longer than broad, diminishing in diameter towards their insertions (Text-figs. 2, 3, 4).

The young empty uterus is short, though proportionally longer than that of the species in Group 1, which deposit undeveloped eggs upon the bodies of their hosts. The tracheation of the organ is less abundant than in the uterus of the Echinomyiine flies. As the eggs accumulate in it, it elongates and rolls up into a flat spiral which fills the abdomen of the female. The eggs lie transversely in juxtaposed series of which there are six in the median part of the organ.

The egg is elongate, with a thin delicate unpigmented chorion. The pneumatic apparatus of the chorion is in the form of a reticulum.

Biology.

No detailed information is as yet available in regard to the time of emergence of the *Digonichaeta* adults in the various localities where it exists. Puparia collected in October 1909 in Denmark gave adults on April 12–24 of the following year according to Nielsen. In 1915 the writer collected puparia in the field during February in various localities in the environs of Cambridge, England. These were placed in an incubator at 25° C. in March, and the adults issued at irregular intervals from March 19 to April 14, the normal time of emergence being probably from the middle to the end of April in the locality in question.

With the exception of Altson, no entomologist has observed copulation and oviposition in *Digonichaeta*. However, in his 1909 paper Pantel concluded from a study of the female reproductive system and the morphology of the primary larva, that the female probably disseminates hatched or hatching larvae in the neighbourhood of the host, an opinion generally shared by subsequent writers on the subject. This theoretical conclusion has been confirmed by the work of Altson (1924) who found that the fly deposits its egg, containing a fully developed embryo, in the immediate vicinity of resting earwigs and that the egg instantly hatches. At what time of year oviposition occurs in the locality in which he worked (Rothamsted Exp. Station, England) Altson does not say, but first-stage larvae still relatively little developed were found by the writer of this paper in young earwigs around Cambridge, England, as late as July 23 in 1915.

As soon as the larva hatches, according to Altson (*l.c.*), it immediately moves off rapidly towards an earwig, mounts its legs and, having discovered a soft spot in the integument in the tip of the abdomen, between the thoracic segments, or as dissections show, more frequently, in the neck, proceeds to bore into the body of the host, leaving its anal segment in the hole by which it penetrated. The proliferation of the hypodermal cells and their reaction to the irritation produced by the larva results in the formation around the body of the latter of an elongate tube, the "integumental sheath" through which the parasite has direct access to the atmospheric air. The larva remains in it feeding on the blood and fat of the host, the consumption of fat being however relatively feeble according to Pantel (1910, p. 112). When the parasite moults, the skin is not pushed down to the posterior extremity but remains in place, lining the interior of the integumental sheath, the first-stage exuvium which

is situated near the neck of the sheath being, as Pantel points out, so perfectly conserved that the structural arrangements are almost exactly as in the first-stage larva.

Towards the end of the third larval stage many Tachinid larvae which have previously contented themselves with the blood and fat of the host, suddenly become sarcophagous, devouring first the fat body and subsequently the other internal organs, so as to leave little but the cuticle.

A minority of species, of which *Digonichaeta* is one, do not exhibit this change in habit, but complete their development on the blood and fat. The emergence of such parasites does not invariably determine the immediate death of the host. We have found on several occasions earwigs from which *Digonichaeta* larvae had emerged and which were still living. They were however very feeble and succumbed in a short time.

As the parasite develops, it bends laterally and extends posteriorly down into the abdomen of the host, so that, although it usually enters in the neck or in the thorax it emerges as a rule from the abdomen either through the soft skin surrounding the terminal appendages or else on the ventral side of the abdomen through the intersegmental conjunctiva. The larval meconium is passed before issuing and remains as an elongate brown curved cylinder in the body cavity of the host. The cylindrical form of the meconium seems to show that a peritrophic membrane really exists in *Digonichaeta*, although we have not been able to discover it in sections of the intestine.

The larva pupates very soon after emergence, usually not far from the body of the host, often under bark in hollow stems, flower heads and other places frequented by the earwigs. The writer has sometimes found under bark, accumulations of issued and unissued puparia, indicating that earwigs and parasites had been living together for several years in the same restricted area.

Seasonal History and Length of Stages.

The length of the various stages in the development of *Digonichaeta* can only be determined by careful experiment which has not as yet been possible.

The larval development is in general very slow especially in the north. In the environs of Cambridge, England, first-stage larvae of *Digonichaeta* were found as early as July 23 and as late as August 23. The following table gives the results of dissections of earwigs from Cambridge in 1915.

Dates	Stage I	Stage II	Stage III
July 23	2	—	—
„ 24	1	—	—
„ 26	1	—	—
Aug. 1	1	—	—
„ 2	2	—	—
„ 7	1	—	—
„ 11	3	—	—
„ 15	—	2	1
„ 16	—	1	—
„ 22	1	4	—
„ 23	1	3	2
Sept. 4	—	4	—

The appearance of first-stage larvae during such an extensive period may be due simply to the fact that oviposition extends in this species over a considerable length of time or it may indicate that the first stage is of unusually long duration in this species. It is of interest in this connection to note that according to Baer (1920–21) *D. setipennis* flies from April to August.

Our data on other localities is less complete. In 1924 freshly formed puparia were found in material from the department of the Orne (N.W. France) on September 18 and 19; in an earwig from Verrières, near Paris, France, a second-stage larva was found on September 18, freshly emerged third-stage larvae and puparia from September 19 to September 22 and even a little later. In material received from Bergamo (Po Valley, N. Italy) freshly formed puparia were found on September 18 and 19.

In the region of Hyères (S. France) in which the climate, of the Mediterranean type, is much warmer and, in the summer months, much drier than any other of the preceding regions, the development of the parasite is in general more rapid and takes place earlier in the year. The observations made in 1923 which are resumed in the following table show very clearly, in comparison with those made at Cambridge, the influence of the warmer climate.

Hyères, France.

Dates	Stage I	Stage II	Puparia
July 7	1	1	—
„ 10	1	—	—
„ 19	1	—	5
„ 20	1	1	—
„ 23	—	—	3
„ 24	—	—	1
Aug. 1	—	—	1
„ 7	—	—	2
„ 13	—	—	13
„ 21	—	—	9
„ 24	—	—	9
„ 28	—	—	17

A more striking effect of climatic conditions on the life-history of *Digonichaeta* is exhibited in the pupal stage. In northern localities, as Pantel (1909) and Nielsen (1912) pointed out, the majority of individuals pass the winter in the pupal condition, but a few emerge before the onset of winter. Out of five puparia collected by Nielsen in October 1909 one fly issued in the same month while the remainder did not emerge until the following April. Similarly one of a number of puparia collected in Cambridge in the autumn of 1915 by the writer emerged in the laboratory in November, while the others did not issue until the following spring. In material from northern regions, as indicated by Pantel, only a very small proportion of the flies emerge in the autumn. Out of over 100 puparia obtained from Bergamo and Northern France in 1921, not one had emerged up to November of that year. It is true that most of these puparia were placed in a refrigerator at 5–10° C. as soon as they were discovered in the breeding trays, but, as will be shown later, there is little reason to believe that the non-emergence was due to the low temperature.

The material reared from earwigs collected at Hyères in 1923 comprised some 60 puparia. These were placed at once in the refrigerator at a temperature of from 10–15° C. Nevertheless, adults began to emerge on July 23 and continued to emerge up to October 31 at irregular intervals, after which the remaining unissued puparia were shipped to the United States. During the period from July 23 to October 31 a total of 18 puparia, or almost a third of those collected, emerged and in all probability others issued after they had been shipped. Had they not been subjected to low temperature from the moment of pupation, a considerable proportion would probably have emerged during the months of July and August.

The premature emergence of these Hyères adults, even under refrigerator conditions, shows that the mode of development characterising any individual puparium is not simply a function of the climatic conditions prevailing during the pupal period. The results obtained with puparia from northern regions brings this out still more clearly. In this case, the majority of the *Digonichaeta* issued from the earwigs after these had been brought to Hyères, during a time (September 19–22) when the mean temperature is 3° C. higher than in the region of Paris. The majority were placed in the ice chest, as already stated, but some were kept at room temperature. None of those kept under observation have emerged up to the date of writing (January 2, 1925). In an attempt to secure premature emergence and reproduction a number of puparia were removed from the ice chest on November 10 and placed in an incubator at 22–28° C.; but none of these gave adults, and dried up without showing any signs of development.

Thus, to resume the observations just cited, in both the northern and southern habitats two types of pupae exist in *Digonichaeta*; the one developing rapidly and issuing as an adult in summer or autumn, the other hibernating until the following spring. The data collected seem to show that the individuals developing in summer and autumn in the southern habitat (Hyères, France—Riviera) are proportionately more numerous than in the northern areas (Denmark, N. France, Holland, England); nevertheless, although the difference in the geographic races is correlated with, and in our opinion probably determined by, the climatic conditions in the two types of habitat, the mere modification of the temperature to which the pupae are subjected will not suffice to annul it. The emergence of individuals of the rapidly developing type cannot be indefinitely retarded by low temperature, nor the emergence of those of the hibernating type induced by high temperature; still less can these types in such manner be transformed one into the other. The difference just mentioned, while perhaps due in the first instance to the climatic conditions which have acted upon the parasites, is in the pupal condition an inherent difference of a profound physiological order.

According to J. Pantel, the double type of nymphosis is most frequent in species adapted to a single host or to a very small number of hosts (monophagous or oligophagous species). The hibernating type he considers to be

manifestly a biological adaptation whose object is to assure the conservation of the species during the winter season, the rapidly developing type apparently utilising such specimens of the habitual or other host as are available towards the close of the year. He could, however, offer no suggestion as to the immediate or efficient cause of the apparition of the pupal types. "On ne voit pas pourquoi," he says (*l.c.* 1910, p. 175), "sur la totalité des individus correspondants à une même date d'empupage et soumis aux mêmes conditions actuelles, quelques-uns soient frappés, à l'exclusion des autres, d'un ralentissement d'évolution à la suite duquel on aura deux dates d'éclosion si distantes."

The recent work of E. Roubaud (1922) on hibernation in non-parasitic Muscids has thrown new light upon this interesting problem.

It has long been known that certain Muscids pass the winter as larvae or pupae, emerging in spring, but this has been generally considered to be due simply to the influence of low temperatures. Pantel's observations on Tachinids, already cited, and those made by the writer of this paper on other species of the same group (1910), indicated clearly enough that, in some cases, hibernation is independent of meteorological conditions. Elsewhere, however, according to Roubaud, it had never been supposed that the winter lethargy of the hibernating Muscids depended on causes other than low temperature. The rise of temperature above a certain critical point was thought to determine the immediate transformation of the hibernating individuals. In 1916 and 1917, however, in studying the biology of *Phormia azurea* and its parasite *Nasonia brevicornis*, Roubaud observed that certain lots of the latter composed of living larvae or pupae could not be induced to issue even when placed in the incubator at 25° C. with plenty of moisture. He later extended his investigations to several species of non-parasitic Muscids and was able to secure some highly interesting data. His general conclusions, which are of great interest, are as follows: There exists among Muscids as among insects of other groups two fairly well marked physiological types, termed by Roubaud *homodynamous* and *heterodynamous*. Certain species such as *Stomoxys calcitrans*, *Musca domestica* and *Drosophila* are able under favourable conditions to reproduce for an indefinite period generation after generation. Low temperatures can produce a momentary suspension of their physiological activity, inducing a form of hibernation from which the insect immediately emerges under the influence of high temperature. These are the *homodynamous* species. Others such as *Lucilia*, *Sarcophaga* and *Mydaea platyptera* are unable to reproduce continuously, generation after generation. After one or more generations in which the individuals develop rapidly there follows a generation characterised by a period of obligatory repose during which the thermic influences which normally accelerate development have no effect. This period of inertia, says the author, may occur either at the end of the larval life (*Lucilia sericata*, *Mydaea platyptera*) or at the beginning of the pupal period (*Sarcophaga falculata*). It is not determined by a fall in the temperature, but is due to an exaggerated accumulation of excretory products, resulting from the antecedent metabolic activity. In the

species which form the *heterodynamous* group, the normal activity of the excretory organs is insufficient to permit of continuous development during an indefinite number of generations. The urinary products accumulate, generation by generation, until there results a condition of intoxication or *asthenia*, inhibiting development. The organisms or elements in this condition—termed by Roubaud *asthenobiosis*—can only resume their physiological activity after undergoing a process of physiological purification. This process, in turn, depends upon the action on the organism of certain reactivating influences. In certain species mere mechanical or physical excitation (burning, bleeding, centrifugalisation, etc.) will induce it. Such is the case in *Lucilia sericata*. In others, such as *Sarcophaga* and *Mydaea* these stimuli are without effect. The most consistently effective reactivating influences, however, are prolonged low temperatures and desiccation, the more important of these two factors being probably the former. According to Roubaud, these two factors, cold and desiccation, in spite of their apparent diversity, determine similar effects because they both produce an arrest of the metabolic activity and, consequently, a decrease in the production of excretory products, particularly urates. Under these conditions, says Roubaud, the task of the excretory organs is facilitated and the excess of waste products little by little eliminated[1]. The periods of hibernation or aestivation thus constitute what the author terms "une cure d'excretion" after which the organism is rejuvenated and able to resume normal activity as soon as environmental conditions are favourable. After one or more generations in which development is rapid, the descendants are again overtaken by asthenia and the phenomena of aestivation or hibernation recur.

A simple explanation can now be found for the curious facts observed by Pantel. As we have seen, this author observed in several species of Tachinidae (*Digonichaeta setipennis*, *Cyrtoplebia ruricola*, *Thrixion halidayanum*, *Gymnosoma rotundatum*) two types of pupal development in material collected at the same time and under similar conditions. The majority of the pupae hibernate, while a few develop rapidly emerging as adults in a few days or at most in a few weeks. According to Roubaud this difference depends simply on the fact that the pupae belong to two different generations. The individuals developing in autumn are the offspring of flies which have been rejuvenated by a resting period, while those which hibernated are the progeny of a summer generation and affected by the hereditary asthenia resulting in heterodynamous species from the accumulation of excretory products after a period of rapid development.

The idea is certainly interesting and cannot for the present be rejected completely, especially in the case of *Digonichaeta*. It may be that in this and the other species mentioned there occurs spring and autumn generations during the time not covered by our observations. The seasonal history would then be somewhat as follows: a majority of the individuals emerge early and reproduce, their offspring issuing in early summer and again reproducing, giving larvae

[1] No explanation is given as to how it is that, under conditions inhibiting the rest of the physiological processes, the excretory system continues to function.

which issue from the host and pupate in autumn, passing the winter in the pupal condition. A minority of the adults emerge late and their offspring issue, pupate and emerge in autumn, reproducing in all probability on adult earwigs. As temperature conditions are unfavourable, they can scarcely complete their larval development in autumn especially since *ex hypothesi* they are now approaching the asthenic condition. They must therefore pass the winter as larvae in the body of the host, issuing and pupating in spring. The larvae found in the dissection of English earwigs, from July 23 to September 4, would thus be a mixture of first and second generation individuals. By means of a few supplementary hypotheses we could easily explain why no evidence of an autumn generation in earwigs has yet been discovered and why the percentage of summer-issuing adults is higher in the Mediterranean zone than in the colder regions.

However, a careful consideration of the available information shows that the problem is somewhat more complex than has been supposed, and that the facts cannot always be explained on the basis of Roubaud's hypothesis in its present form; as Picard has already pointed out. In our opinion, the difference noted in the life-history of *Digonichaeta setipennis*, in the climatically different parts of its range, are probably somewhat similar to those existing in such insects as the European corn borer. In the warmer regions, where the parasite develops rapidly, a considerable number emerge after a short pupal period. In the cooler zones, where development is slow, the great majority hibernate in the pupal stage. That these differences are due to climatic factors seems scarcely open to question. Just how they operate is, however, uncertain and must remain so until our knowledge of the life-history of *Digonichaeta* in the various parts of its range is complete. The simplest interpretation of the data now available, in terms of Roubaud's suggestion, would be that conditions which tend to retard metabolism and lengthen the period of development, notably perhaps low temperatures, produce intoxication and asthenia in the individual of the heterodynamic species, while factors determining rapid development produce also a more complete elimination of excretory products, although the asthenic condition ultimately supervenes in the descendants after one or more generations. It may be, however, that the seasonal history is predetermined in the egg and that the factors which are effective in determining the length of the larval and pupal stages are those which operate during the winter months on the hibernating pupae. Extensive further researches would be necessary in order to elucidate the problem.

Hosts of Digonichaeta setipennis.

As has already been stated, the most important host of this species is *Forficula auricularia* L. It has not been recorded from the other earwigs and was not found by the writer in either *Labia minor* L. or *Anisolabis moesta* G. On one occasion, however, a larva of this species was found in a specimen of *Chelidura albipennis* Meg.

The parasite is also recorded from a number of Lepidopterous larvae such as *Pheosia tremula* Cl., *Lasiocampa quercus* L., *Euproctis chrysorrhoea* L., *Notodonta trepida* Esp., *Panolis griseovariegata* Goeze, as well as from caterpillars of the Microlepidoptera *Dioryctia abietella* F., *Grapholitha strobilella* L. and *Carpocapsa pomonella* L. These are considered by Baer to be alternate hosts. "This insect," says Altson, "has been recorded from other hosts of no less than four orders, including Lepidopterous larvae; this may be explained by the fact that earwigs hide away in an endless variety of situations during the day, and the Tachinid larva in its search for its host has happened upon an accidental one that has had the misfortune to cross its path."

In the opinion of the present writer, the record of rearings from hosts other than the earwig, while not absolutely negligible, requires verification, as it seems unlikely that a parasite with a host relation as specialised as is that of *Digonichaeta* could complete its development successfully in insects of other groups. The possibility of this could easily be determined experimentally.

Geographical Distributions.

The distribution of this species is given by Bezzi and Stein as "Europe." We have reared it from earwigs in England, Northern and Southern France (Hyères) and Northern Italy (Po Valley). Nielsen found it commonly in Denmark. It is recorded also from Sweden, Finland, Germany, Austria and Russia, and is probably generally distributed throughout Europe.

Nothing is known at present as to the relative abundance of the species in the various portions of its range nor in regard to the factors which determine the local distribution.

Hyperparasites.

I reared in England from this species an undetermined Tetrastichine. Altson records the common Chalcid *Dibrachys boucheanus* Ratz. as well as the Ichneumonid *Phygadeuon scaposus* Thoms. which he thinks attacks the parasite while it is still within the earwig.

Messrs H. C. Atwell and H. C. Stearns state in an unpublished report on the *Digonichaeta* material collected in England during the winter and shipped by Dr H. L. Parker and the present writer to Oregon that of 443 puparia 46, or 10·4 per cent., gave *Phygadeuon scaposus*, while 2, or 0·45 per cent., gave *Dibrachys boucheanus*.

IV. *Rhacodineura antiqua* Meig.

Larva, Stage I (Pl. VIII, figs. 28, 29, 30).

Egg 0·13 mm. by 0·10 mm. approx.; larva 0·142 mm. by 0·095 mm. approx. (larva surrounded by the vitelline membrane).

The material in my possession comprises only somewhat immature larvae.

Skin transparent and colourless without any cuticular specialisation excepting for the usual spines. Sensorial organs minute, the antennary organ broader than long.

On segment I, a dorsal group of six large hooks (Pl. VIII, fig. 27), the bases of which are narrow and elongate (l. about 0·144 mm.), the other hooks of this segment feeble, with the exception of some short and stout elements on the ventral surface; on the anterior margin of segment II, a row of rather feeble hooks whose base is often narrow and elongate; behind the second segment, the form of the spines is difficult to make out, but there appear to be 8 or 9 complete bands each composed of a single row of rather feeble spines situated on the anterior margin of the segments.

Larva apneustic, neither felt chambers nor spiracles visible in the specimens I have examined. The buccal armature (Pl. V, fig. 11) is small (l. 0·054 mm.) and differs greatly from that of *D. setipennis*. The anterior ventral tooth is large and very broad, its breadth and its base being equal to the length of its anterior margin; there is no distinct angle between its posterior border and the inferior edge of the remainder of the anterior region; the accessory dorsal tooth is acute, sometimes almost as long as the lower tooth, its lower border making with the anterior border of the ventral tooth a broadly open angle; upper border of the anterior region slightly convex, only a little longer than the distance between the apex of the dorsal tooth and that of the ventral; the height of the anterior region at its base equal to about half this distance, the distance from the anterior extremity of the dorsal border of the intermediate region to the space separating the dorsal and ventral wing plates, about $1\frac{1}{2}$ times the length of the dorsal border of the anterior region; ventral wing plate short, indistinct; dorsal plate elongate, straight, acute at end, almost as long as the anterior region; sclerite of the salivary duct indistinct, anterior lateral plate vaguely triangular in form.

Larva, Stage II.

Dimensions: l. 1·25 mm., w. 0·5 mm. approx.

The cuticula is colourless; segments I and II bear on their anterior borders 2 or 3 rows of fine spines; the ventral region of segment XI between its anterior border and the posterior spiracles is also studded with fine spines; elsewhere the cuticle is apparently glabrous.

No anterior stigmata are visible; the posterior stigmata are present, with short, broad, piriform felt chambers of a type not infrequently present in larvae which are apneustic in stage I.

The antenna is minute and inconspicuous, broader than long; no other sensoria are visible.

The mouth-hook (Pl. IX, fig. 44) (l. 0·148 mm.–0·172 mm.; of the anterior hook from base to apex, 0·096 mm.; height of intermediate region at level of the sclerite of the salivary gland, 0·028 mm.) of the second-stage larva is very different from that of the first and third stages, being characterised by the very elongate slender paired anterior hooks; these hooks, whose bases are enlarged into a blunt downwardly directed ventral tooth and a moderately acute, backwardly directed dorsal tooth, are equal in length to the intermediate and

posterior regions taken together; the anterior and intermediate regions are separated by a distinct interval and connected only by a narrow bridge of chitin; the intermediate region is very short, the basal region relatively small, with the dorsal wing very little longer than the ventral wing, the interalar space acute anteriorly; the anterior hooks seen from above are not parallel but strongly divergent from the base forward.

Larva, Stage III.

According to Nielsen the length is from 4·5 to 10·0 mm.; my specimens were about 8·0 mm.

The cuticula is said by Nielsen to be absolutely glabrous but, as Pantel has already pointed out, this is incorrect; numerous short colourless appressed spines are present, though they are inconspicuous because of their minuteness and lack of pigmentation. Segment I is not visible in my specimens; the anterior border of segment II bears a band of spines comprising 8–10 rows on the ventral surface and about 10 rows on the dorsal surface; on the anterior border of segment III the band is narrower with only 4–6 rows; these spines are posteriorly directed, but there are several rows of anteriorly directed spines on the posterior border of the segment, especially in the pleural regions, where they are arranged in rings around the fontanelle of the pupal respiratory cornicle, all the elements in this area being directed away from the place where the cornicle traverses the wall of the puparium; segment IV bears an anterior band much like that on segment III; segments V–IX inclusive bear both anterior and posterior bands, comprising each 3 or 4 rows of spines, the anterior ones directed posteriorly, the posterior ones directed anteriorly; segment XI bears some spines behind the anal opening and others around the stigmatic areas.

The *buccopharyngeal armature* (Pl. VIII, fig. 25) differs almost as much from that of the second stage as the latter does from that of the first stage, all the sclerites being unusually short and stout, whereas those of the first stage are long and slender (l. 0·50 mm., m. hook, base to apex, 0·16 mm., int. region, 0·119 mm., basal region, dorsal wing, 0·143 mm., ventral wing, 0·154 mm.). In this stage a distinct articulation appears to exist between the intermediate and basal region, but the intermediate region is fused in front with the base of the mouth hook, although there is a well marked constriction at the point of junction. The "mandibular sclerites" are broad with a short recurved apical portion, sub-acute at the tip; ventrad of their bases lies a heavily chitinised hypopharyngeal plate very similar to what has been described in *Digonichaeta* but which does not seem to bear spines; it is provided anteriorly with a pair of large circular sensoria, posteriorly with a pair of small ones of the same form. The upper border of the intermediate region is deeply emarginate in its posterior half and the anterior border of the basal sclerite which surrounds the intermediate sclerite posteriorly is dorsally bifurcated so as to fit around the dorsal tooth-like portion.

The dorsal wing of the basal sclerite, which is more feebly chitinised than

the anterior and intermediate regions, is broad, somewhat longer than the ventral wing which is bifurcate posteriorly, the dorsal part being narrow and acute posteriorly, the ventral part broad and posteriorly truncate.

The anterior stigmata (Pl. IX, fig. 41), which are situated on the posterior border of segment I are slightly protuberant but minute, the apex flattened, its long axis parallel to the border of the segment. The atrium or felt chamber is elongate and cylindrical, its apex terminating in a rounded conical rather strongly pigmented and chitinised cap. The number of respiratory papillae, says Nielsen, shows a greater variability than he had observed in any Muscid larva. In some larva there is only a single respiratory papilla, more frequently two and in some instances as many as four; Nielsen points out that the increase in the number of the papillae is not correlated with an increase in size of the tip of the felt chamber; as the papillae increase in number they diminish in size. The posterior spiracles resemble considerably those of *Digonichaeta*, the respiratory areas being situated at the end of a pair of strongly protuberant elongate black sub-cylindrical peritremes (Pl. IX, fig. 39).

The form and disposition of the respiratory slits is very characteristic; instead of about 10 elongate slits radiating from the moulting scar of the spiracular area as in *Digonichaeta* there are about 30 short slits disposed side by side in the peripheral part of the respiratory area as shown in our figure.

Puparium (Pl. IX, fig. 37).

Dimensions: 5 mm. × 2 mm. to 6 mm. × 3 mm. Colour yellowish red, sub-shining, more cylindrical than *Digonichaeta*, rounded anteriorly and posteriorly; spiracles situated on the posterior extremity of the longitudinal axis, elongate, black, more or less divergent but separated at base by a distance equal to the basal diameter of one of them, anal opening situated on the under side at the anterior border of segment XI, its distance from the base of the stigmatic tubercles a little greater than the length of the latter; anterior spiracles minute but usually a little more conspicuous than in *Digonichaeta*. The pupal respiratory system (Pl. VIII, figs. 34, 35) is complete, the prothoracic cornicles are well developed with a rather small number of respiratory orifices; the internal spiracles with over 100 respiratory papillae arranged on 7 or 8 radiating branches at the end of the atrium.

Internal Anatomy of the Larva.

The anatomy of the larva of *Rhacodineura antiqua* is very remarkable and in some respects apparently unique among Tachinid larvae. The material at the disposal of the present writer is unfortunately insufficient to permit of a detailed study which is very desirable.

The *intestine* is convoluted without any distinctly enlarged region such as is present in *Digonichaeta*; the diameter of the oesophageal valve does not exceed that of the mid-intestine; two gastric caeca are present, having the form of rudimentary evaginations as in most Tachinids where caeca exist; the fat globules in the cells of the mid-intestine are yellow, while those of the adipose

tissue are colourless; the *Malpighian tubes* are enormous in diameter in comparison with the size of the larva, with huge cells; the posterior pair lie in the posterior part of the body; the anterior pair extend forward into segment V where they bend abruptly and run backward into segment VII, the recurrent portion being thin-walled as in the majority of Tachinid larvae; the *salivary glands are* short and broad, extending only to the posterior border of segment V; only 4 *oenocytes*, situated in segments IV and VI are to be found on each side of the body; but though few in number they are of great size; the finer *tracheae* and *tracheoles* lack the special thickening usually present, being moniliform, as in certain other Tachinid larvae, for example, *Sturmia scutellata* R.-D.; the genital glands lie in segment VIII; the *dorsal vessel*, of which Pantel (1914) has given a full description, is very remarkable; the cardiac region comprises only two chambers instead of three as is the rule in Tachinid larvae, but the posterior chamber, instead of being closed posteriorly is provided with a terminal unpaired ostiole with strongly invaginated lips constituting functional valves. The parietal cells of the ventricular chambers and of the chambers of the intermediate region are 2 in number on each side, instead of 4, as is usual. The wall of the chamber which precedes the heart is transformed on each side into a proventricular pad so as to form an intraventricular valvule preventing the reflux of the blood during diastole.

The *pericardial cells* are reduced in number, only 3–4 being present on each side.

The *muscular system* could not be accurately studied because of lack of material; it seems to resemble in its general character that of *Digonichaeta*, but there is apparently a reduction in the number of the fibres in certain places (muscle 19 in *Miltogramma* (Pl. VII, fig. 22) is absent; the dorsal recti-muscles 1–3 seem to be fused; the fibres are in general feeble).

The *imaginal discs* of the limbs are unusually stout.

As pointed out by J. Pantel, this species is characterised by a general reduction in the number of the cellular elements of the various tissues, the deficiency in this respect being compensated by the large size of the individual elements. The adaptive significance of this peculiar feature is quite obscure, since it characterises neither life in the earwigs (being absent in *Digonichaeta*) nor the other larvae of the type depositing eggs on leaves.

Reproductive System of Adult Female.

The reproductive system of the adult female has not yet been studied in detail. According to Pantel (1910) the ovarioles contain a series of mature eggs above which there is only a somewhat indistinct young chamber and the terminal chamber, which indicates that all the eggs deposited by the female reach maturity about the same time. The uterus is voluminous and abundantly provided with tracheae, destined in the opinion of Pantel to furnish a supply of oxygen for the developing larvae.

The *egg* (Pl. VIII, figs. 28, 29, 30), like all those destined to be deposited upon

food of the host, is plano-convex, the lower surface being thin and transparent, the upper thick and pigmented; but what especially characterises this egg and distinguishes it from those of the other species of the group is that the upper surface, instead of being regularly rounded, is in the form of an asymmetrical cone, whose apex is composed of an irregular group of rounded protuberances. In the zone surrounding the base of this part of the egg there is a considerable number of minute button-like structures, more or less oval in outline, the form of which, seen from the side, resembles somewhat the fructifications of certain lichens. These structures probably constitute the respiratory apparatus of the egg.

Biology.

The data available on the biology of this species are as yet somewhat incomplete.

It has long been suspected that *Rhacodineura antiqua* deposits its eggs upon the food of the host. In his paper in the *Horae Societatis Entomologicae Rossicae* for 1897, Rodzianko discussed in detail the method of penetration of the parasite. After mentioning the methods of attack then known in the Tachinidae, he refers to the biology of *Crossocosmia sericariae* Rdi. as described by Sasaki and then sets forth in order the facts he considers of special significance in formulating a hypothesis in regard to the oviposition of *Rachodineura*. He points out that although the female of the parasite deposits a large number of eggs the parasitism is very low, that the larvae of the earwig are very mobile and have the habit of cleaning the body and limbs frequently; that the fly is diurnal whereas the host is nocturnal; that the earwigs frequently devour insect eggs and, finally, that the eggs of *Rhacodineura* are very minute. Although Rodzianko's prudence prevented him from formulating this hypothesis definitely, his arguments obviously lead to the conclusion that the parasite deposits its eggs upon the food of the host. The fact that his remarks upon the aspect of the matter are to be found only in the Russian text has prevented the author from receiving due credit for his suggestion, which was advanced as new by J. Pantel in 1910. This author placed *R. antiqua* (discussed by him under the name of *Ceromasia rufipes*) in the group of species depositing eggs upon the food of the host, on the characters of the female reproductive system and the egg and was followed on this opinion by subsequent authors including the present writer. It was not until 1924, however, that definite observations as to the oviposition were published by Altson, who states that the fly is found to lay a minute egg containing a fully developed larva on anything that earwigs have fed upon in the previous night, which indicates that a preliminary contact betweeen host and food material is necessary in order to determine oviposition by the parasite. The eggs are swallowed by earwigs coming out to continue their unfinished meal. In the experiments, flowers, foliage, fruits and vegetables were available for the oviposition of the flies.

The eggs hatch in the alimentary tract. Egg cases were found in the pellets of excrement, about 24 hours after being swallowed. The first-stage larva has

not up to the present been found in the host by any investigator, possibly because of its minuteness. During the early part of the second stage it lives free in the body cavity but later moves to the neck of the host, which it punctures. Altson apparently considers that the larva utilises its mouth hook to perforate the integument, after which it turns and fixes its anal plate to the opening; but it seems to the writer more probable that, like other Tachinid larvae which pass the latter part of their lives in secondary integumental sheaths, the parasite makes the opening simply by thrusting its posterior extremity against the skin. The sheath which forms around the larva, according to Pantel (1916), closely resembles the primary integumental sheath of *Dagonichaeta*. During a certain period it completely envelops the body of the parasite, which moults a short time after fixation, the moult skin remaining within the sheath. When the larva approaches maturity, it bursts through the sheath and may then attack the fat body of the host. The normal food of the parasite is blood and fat. After emerging from the sheath the larva issues from the earwig through the soft membrane between the abdominal segments or around the terminal organs of the abdomen. As Rodzianko pointed out, the host may survive for several days after the emergence of the parasite, but eventually dies of exhaustion and shock. The parasite thus does not pass through a sarcophagous stage and in this respect it resembles *Digonichaeta*. Pupation takes place under bark or in any other situation, not necessarily in earth. The pupal stage requires, according to Pantel, 16–38 days, according to Rodzianko, 16–19 days.

The seasonal history apparently varies considerably in the various regions inhabited by the species, as does that of *Digonichaeta*. In England, according to Altson, the larvae which enter the earwigs in spring require from 10 to 12 months to complete their development, hibernating in the second stage in the body of the host and emerging to pupate in the spring. Pantel states that he has found the second-stage larvae in July (Gemert, Holland) August (Gemert, Setubal (Portugal), Neffies (S. France)), September (Setubal), January (Vals (Central France), Sarria (Spain)), March (Gemert), May (Gemert, Setubal).

He considers that in any locality where adult earwigs exist the year round, the parasite could also be found practically at any time, mainly as a second-stage larva. The third-stage larva, he says, is only found around the time of the emergence of the adult; in January (Sarria), April (Tortosa (Spain)), June (Gemert), August (Neffies). Rodzianko found *Rhacodineura* in earwigs at Poltava in S. Russia in March, April and May but on one occasion obtained a puparium from earwig larvae collected in September, from which the adult issued in November. The only specimens we have reared up to the present were secured from earwigs collected at Bergamo in Northern Italy in August. The larvae from these specimens issued to pupate not long after collection and emerged as adults in the autumn of the same year. From living earwigs collected in England during the winter months, and shipped to the Western

United States, larvae issued to pupate in spring. It seems probable that more than one generation per annum occurs in certain districts.

The geographical range of *Rhacodineura antiqua* seems to be very extensive since it has been found from Copenhagen in the north to points in Spain and Portugal in the south and from Russia in the east to England in the west. It is evidently capable of existing in a great variety of climatic zones and should attack the earwig wherever the latter becomes established, though it is in Europe much less common than *Digonichaeta setipennis*.

V. *Digonichaeta* and *Rhacodineura* as Controlling Factors of the Earwig.

As the European earwig has been accidentally introduced into the United States (Portland, Oregon and Newport, Rhode Island) and New Zealand (Central Otago) and has become a rather serious pest in these regions, the problem of its control has assumed a certain importance. It is therefore interesting to consider briefly the rôle of the parasites described in this paper as controlling factors of the earwig.

The effect exerted by the ordinary entomophagous parasite on its host is twofold. The first is the effect on the general metabolism produced by the presence of the parasite within the body of its host, whereby the activity of the latter may be diminished and the damage it occasions thereby reduced. That parasites sometimes produce this effect has been demonstrated by Crossman (1922) who showed in his excellent study of *Apanteles melanoscelus* R., that parasitised larvae of *Poarthetria dispar* L. consume somewhat less food than unparasitised larvae. Whether the parasites of the earwig affect it in this way is uncertain.

The second effect produced by a parasite is in limiting the increase of the species by killing the host before it is sexually mature. *Digonichaeta* and *Rhacodineura* both emerge from the adult earwig but usually cause the death of the host before it has reached the age when it would normally oviposit. It is in any event improbable that many earwigs containing parasite larvae could ever reproduce, because the presence of the parasites determines a partial atrophy of the reproductive organs. A comparison of Pl. IX, figs. 42 and 43, representing the ovaries of parasitised and unparasitised earwigs will give an idea of the effect which the presence of the parasite may produce.

The limitation of the rate of increase produced by the parasites by the death or parasitic castration of their hosts, depends, as has been shown at length in another paper (Thompson, 1928), *on the fraction of the total population which they destroy and for the destruction of which they are indispensable.*

Considered from this angle, the effect exerted by *Rhacodineura* and *Digonichaeta* upon the earwig in its native home does not seem to be of enormous importance. In no earwig collections we have made in any part of Europe has the mortality from *Digonichaeta* exceeded 10 per cent. of the population present while the mortality from *Rhacodineura* has been less than 1 per cent.

It must be noted further, that this mortality is calculated in respect to the population present at the time of observation. A great many earwigs die off in the younger stages from non-parasitic causes, to which the natural control of the insect is probably mainly due. The fraction of the total population existing at the beginning of any given generation destroyed by the parasites is probably much less than 1 per cent. Furthermore, other causes of mortality may act at the same time, and produce approximately the same effect, whether the parasites are present or not.

No indication that the parasites are able to increase to the point where they will exterminate the host population has ever been observed. In spite of the ingenious adaptations of these Diptera, their life in association with the earwig is apparently precarious and though they suffer relatively little from the attacks of secondaries they are apparently unable to dominate their host. Whether they will play a more important part in the control of the earwig in the new environments to which it has spread, experiment alone can determine.

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EXPLANATION OF PLATES IV—IX.

PLATE IV.

Fig. 1. *Digonichaeta setipennis* Fall. Head of adult, from the side.

Fig. 2. *Rhacodineura antiqua* Meig. Head of adult, from the side.

Fig. 3. *Digonichaeta setipennis* Fall. Wing of adult.

Fig. 4. *Rhacodineura antiqua* Meig. Wing of adult.

Fig. 5. *Digonichaeta setipennis* Fall. First-stage larva, *in toto*, dorsal view.

Fig. 6. *Digonichaeta setipennis* Fall. Head of first-stage larva and first segment, greatly enlarged. *o.a.*, antennary organ; *o.pa.*, pre-antennary organ; the arrangement of the setiform and ring-shaped sensoria of the dorsal half of the first segment is shown.

Fig. 7. *Digonichaeta setipennis* Fall. Pupal respiratory apparatus (internal spiracle).

PLATE V.

Fig. 8. *Digonichaeta setipennis* Fall. Buccopharyngeal armature of first-stage larva, in dorsal view.

Fig. 9. *Digonichaeta setipennis* Fall. Buccopharyngeal armature of first-stage larva, in lateral view.

Fig. 10. *Digonichaeta setipennis* Fall. Dorso-ventral longitudinal section of first-stage larva, showing lobe on anterior end of ventral nerve mass.

Fig. 11. *Rhacodineura antiqua* Meig. Buccopharyngeal armature of first-stage larva, in lateral view; the dark patch on the anterior hook is one of the paired anterior lateral plates.

Fig. 12. *Digonichaeta setipennis* Fall. Last segment of first-stage larva, in dorsal view, showing sensoria, cuticular armature and posterior spiracles with their felt chambers.

Fig. 13. *Digonichaeta setipennis* Fall. Last segment of first-stage larva, showing sensoria and cuticular armature.

Fig. 14. *Digonichaeta setipennis* Fall. Buccopharyngeal armature of second-stage larva, lateral view, showing the chitinised lower lip with its muscle.

Fig. 15. *Digonichaeta setipennis* Fall. Chitinised lower lip or hypopharyngeal plate of third-stage larva, showing the reticulum and spines together with the ring-shaped sensoria near the posterior border.

PLATE VI.

Fig. 16. *Digonichaeta setipennis* Fall. Buccopharyngeal armature of third-stage larva.

Fig. 17. *Miltogramma punctatum* Meig. Buccopharyngeal armature of third-stage larva. *c.m.*, mandibular hooks; *s.d.*, "dentate sclerite"; *p.h.*, hypopharyngeal sclerite; *p. en H.*, H-shaped sclerite; *p.c.s.*, sclerite of the salivary duct; *p.a.d.*, dorsal accessory sclerite; *p.b.*, basal sclerite. Compare this free-living form with the parasitic forms here described.

Fig. 18. *Digonichaeta setipennis* Fall. Buccopharyngeal armature of second-stage larva, ventral view. *c.l.*, lateral or mandibular sclerites, here fused with the posterior portion of armature; and united by a band of chitin; *p.b.*, basal sclerite; *p.e.*, epipharyngeal sclerite; *p.h.*, hypopharyngeal sclerite; *p.H.*, H-shaped sclerite.

Fig. 19. *Digonichaeta setipennis* Fall. Dorso-ventral section of anterior part of second-stage larva, made longitudinally, showing the chitinised lower lip with its muscle; above the armature, the bulb of the antennary organ; below, the bulb of the hypopharyngeal sensoria, the salivary duct and, in lower right-hand corner of figure, an imaginal disc of one of the legs.

Fig. 20. *Digonichaeta setipennis* Fall. Transverse section of second-stage larva in the anterior region. *oe.v.*, oesophageal valve; *v.n.m.*, ventral nerve mass; *m.t.*, Malpighian tubules; *m.i.*, mid-intestine; *a.i.*, adipose tissue; *s.g.*, salivary glands.

Fig. 21. *Digonichaeta setipennis* Fall. Digestive system of second-stage larva, *in toto*, with nervous system and pharynx. *p.*, pharynx with buccopharyngeal armature; *i.m.h.*, imaginal discs of head; *c.g.*, cerebroid ganglia; *v.n.m.*, ventral nerve mass; *oe.v.*, oesophageal valve; *m.i.*, mid-intestine with enlarged stomach-like posterior portion; *m.t.*, Malpighian tubules, *a.*, anterior, *p.*, posterior; *h.i.* hind-intestine.

PLATE VII.

Fig. 22. *Miltogramma punctatum* Meig. Integumental muscular system of two abdominal segments of third-stage larva, from the left side, seen from within. *D*, *V*, *A*, *P*, dorsal, ventral, anterior and posterior directions; 1–4, dorsal recti-muscles; 5–9, oblique dorso-lateral muscles; 10, pleural recti-muscle; 11, oblique pleural muscle; 12, intersegmental circular muscle; 13, intrasegmental circular muscle: 14–17, pleuro-ventral recti-muscles; 18, trifurcated oblique pleuro-ventral muscle; 19–22, oblique pleuro-ventral muscles; 23–25, oblique ventral muscles; 26, circular pleuro-ventral muscle; *ph.* 1–3, hypodermic plates (histoblasts of imaginal integument); *s.n.f.*, non-functional spiracles: this arrangement of the muscles and other organs differs in only a few points from the arrangement in *Digonichaeta setipennis* Fall.

Fig. 23. *Miltogramma punctatum* Meig. Musculature of buccopharyngeal system of third-stage larva, lateral view. *c.g.c.*, cells generating the anterior hook; *d.i.*, imaginal disc; *d.m.*, depressors of the mouth hooks; *e.l.s.*, elevators of the upper lip; *e.m.*, elevators of the mandibular hook; *p.d.c.*, dorsal cephalic protractor; *p.v.c.*, ventral cephalic protractor; *a.p.*, pharyngeal depressor (Hewitt); *r.d.p.*, dorsal pharyngeal retractors; *s.d.*, "dentate sclerite"; N.B. the muscle-like band behind *p.v.c.* is simply a fold of the dorsal pharyngeal sac which exists in this species.

Fig. 24. *Miltogramma punctatum* Meig. Musculature of buccopharyngeal system of third-stage larva, ventral view. *c.g.c.*, cells generating the anterior hook; *d.i.*, imaginal disc; *d.m.*, mandibular depressors; *l.i.*, lower lip; *r.l.i.*, retractors of the lower lip; *m.g.s.*, muscle of the salivary duct; *p.v.c.*, ventral cephalic protractors: compare with Pl. V, fig. 14; Pl. VI, figs. 18 and 19, of *Digonichaeta setipennis*.

PLATE VIII.

Fig. 25. *Rhacodineura antiqua* Meig. Buccopharyngeal armature of third-stage larva, lateral view.

Fig. 26. *Digonichaeta setipennis* Fall. Antennary and pre-antennary organs of second-stage larva with their nerve bulbs, showing that the pre-antennary organ is part of the maxillary complex. *a.*, antennary bulb; *m.*, maxillary bulb.

Fig. 27. *Rhacodineura antiqua* Meig. Hooks from cuticula of anterior extremity of first-stage larva.

Fig. 28. *Rhacodineura antiqua* Meig. Egg, lateral view.

Fig. 29. *Rhacodineura antiqua* Meig. Respiratory papillae from egg, seen from above.

Fig. 30. *Rhacodineura antiqua* Meig. Respiratory papillae from egg, seen from side.

Fig. 31. *Digonichaeta setipennis* Fall. Epipharyngeal plate of third-stage larva, showing sensoria.

Fig. 32. *Digonichaeta setipennis* Fall. Last segment of first-stage larva, in optical section lateral view, showing end of intestine and anal opening, ventral pseudopod of last segment with its muscle, tracheal trunk, felt chamber and spiracle, and principal setiform sensoria. *h.*, hind-intestine; *t.*, trachea; *p.*, pseudopod.

Fig. 33. *Digonichaeta setipennis* Fall. Anterior spiracle of second-stage larva.

Fig. 34. *Rhacodineura antiqua* Meig. Pupal respiratory apparatus. *r.c.*, respiratory cornicle; *i.sp.*, internal spiracle.

Fig. 35. *Rhacodineura antiqua* Meig. Pupal respiratory apparatus. Tip of the respiratory cornicle, more highly magnified, to show the respiratory openings.

PLATE IX.

Fig. 36. *Digonichaeta setipennis* Fall. Posterior extremity of puparium, ventral view, showing posterior stigmata and anal opening.

Fig. 37. *Rhacodineura antiqua* Meig. Posterior extremity of puparium, ventral view, showing posterior stigmata and anal opening.

Fig. 38. *Digonichaeta setipennis* Fall. Third-stage larva in sagittal section to show form of nervous system in this stage.

Fig. 39. *Rhacodineura antiqua* Meig. Posterior stigmata of third-stage larva, showing arrangement of the spiracular slits.

Fig. 40. *Digonichaeta setipennis* Fall. Posterior stigmata of third-stage larva, showing arrangement of the spiracular slits.

Fig. 41. *Rhacodineura antiqua* Meig. Anterior stigma of third-stage larva, showing the variations in its form (from Nielsen).

Fig. 42. Ovaries of adult female of *Forficula auricularia* L., containing third-stage larva of *Digonichaeta setipennis* Fall.

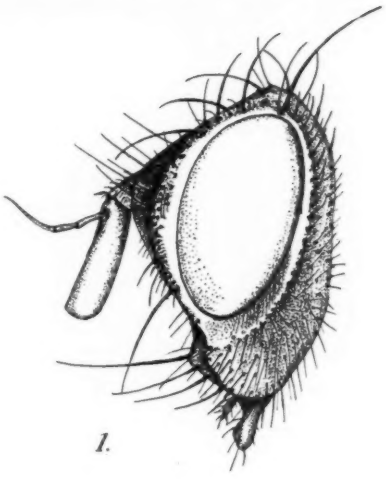
Fig. 43. Ovaries of unparasited adult female of *Forficula auricularia* L. under same magnification as those of Fig. 42.

Fig. 44. *Rhacodineura antiqua* Meig. Buccopharyngeal armature of second-stage larva, lateral view.

Fig. 45. *Digonichaeta setipennis* Fall. Felt chambers and posterior stigmata of second-stage larva.

Fig. 46. *Digonichaeta setipennis* Fall. Felt chamber and anterior stigma of third-stage larva.

(*MS. received for publication* 19. XII. 1927.—Ed.)



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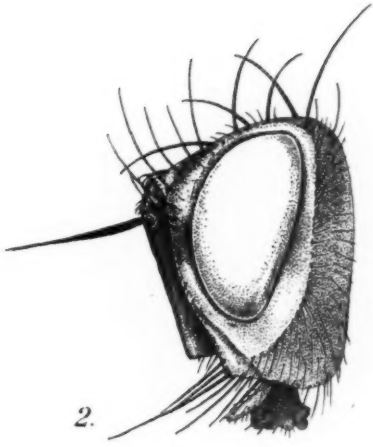

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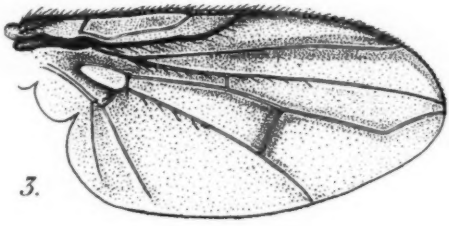

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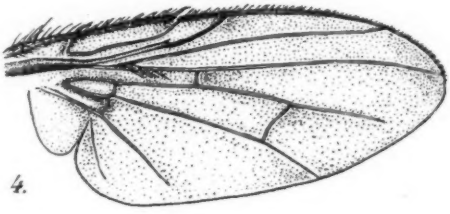

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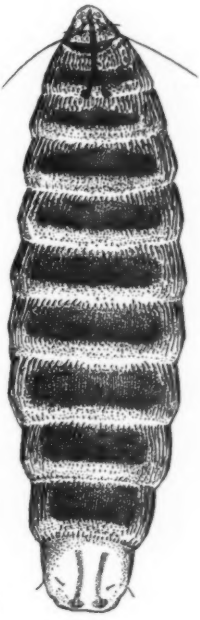

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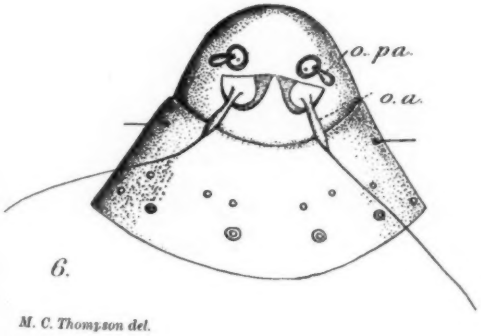

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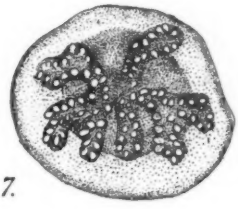

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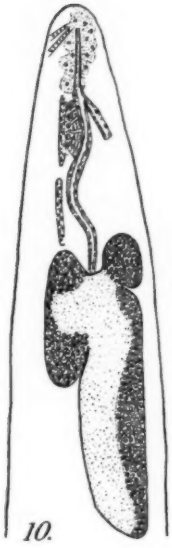

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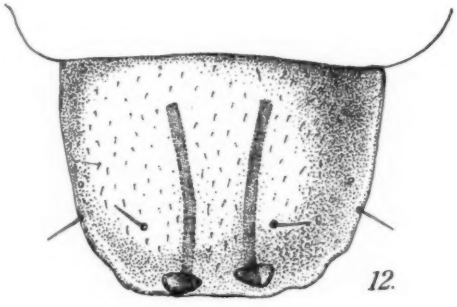

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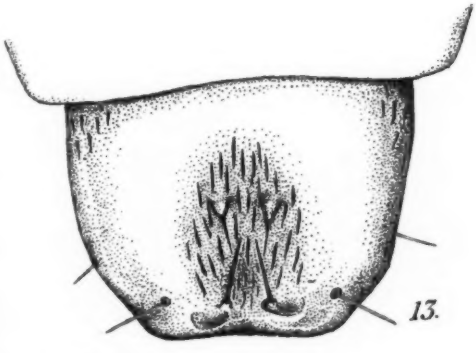

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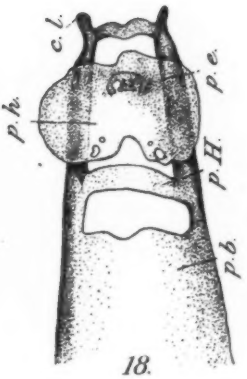

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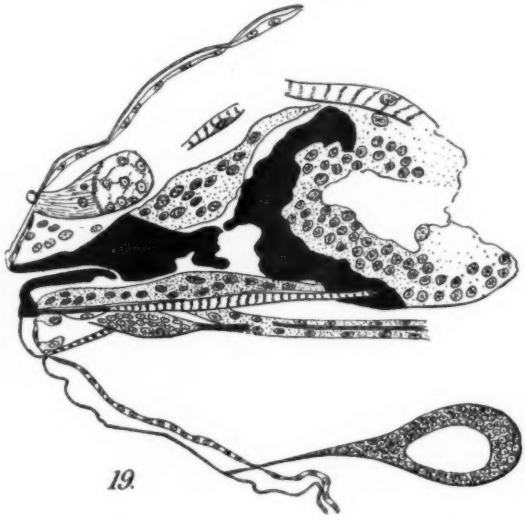

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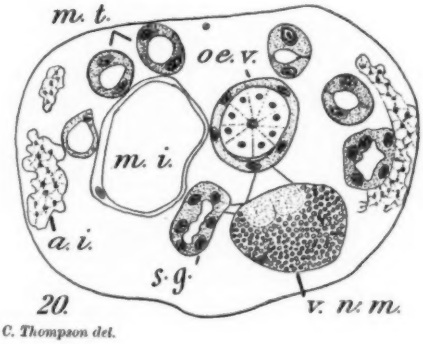

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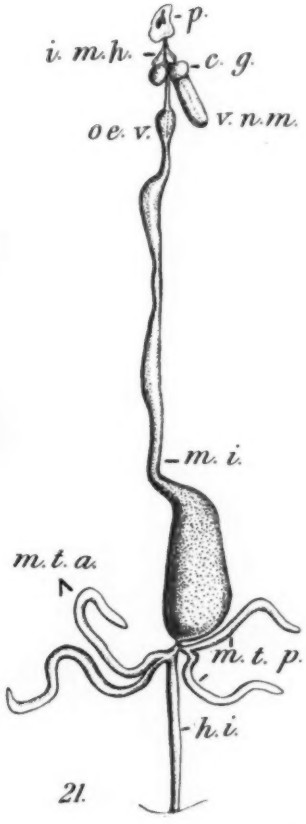

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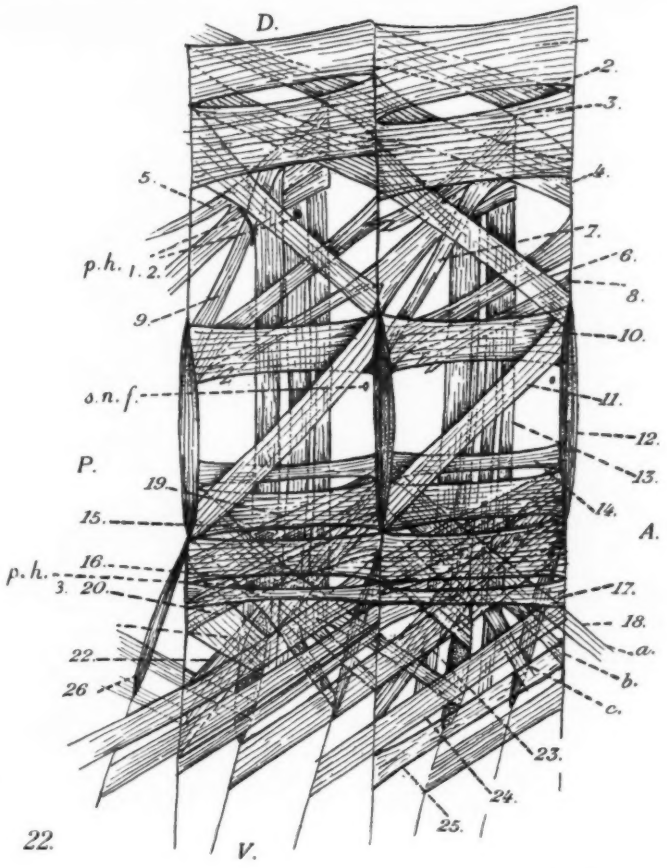

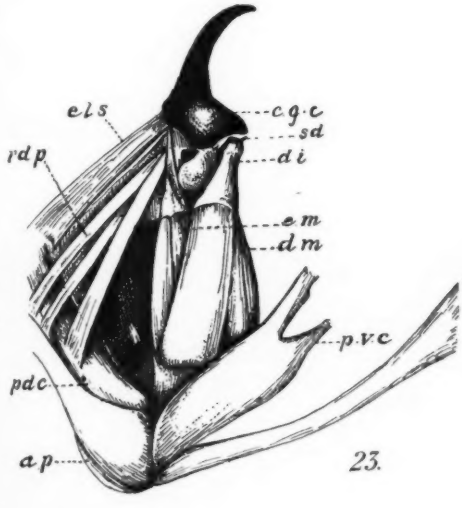

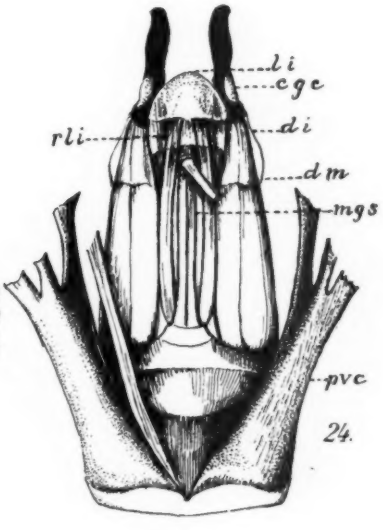

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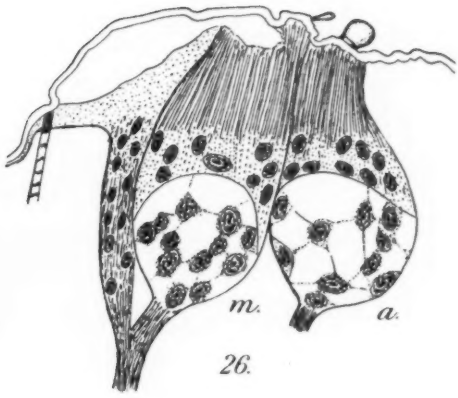

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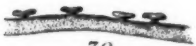

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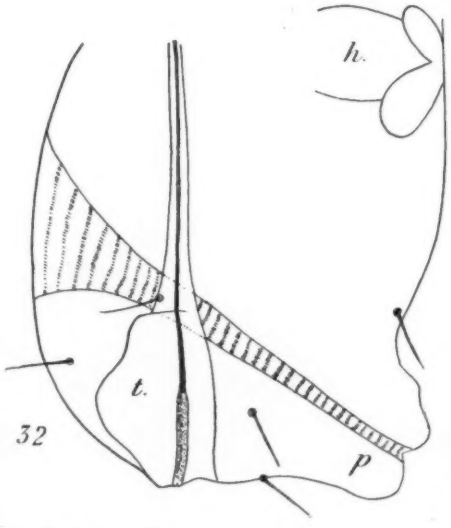

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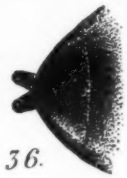

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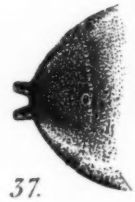

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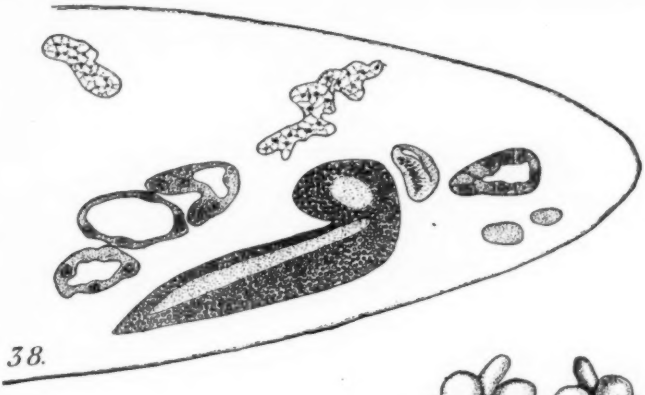

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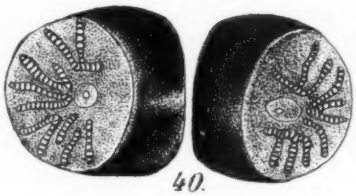

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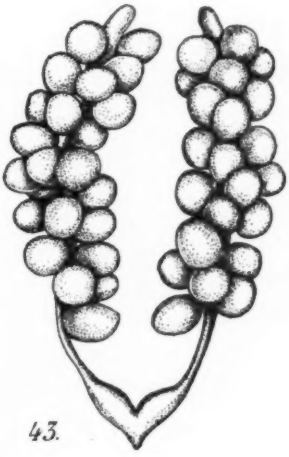

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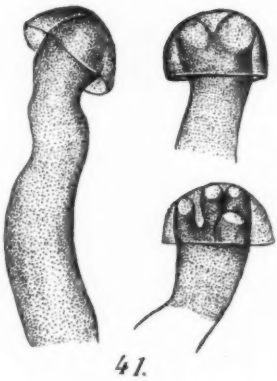

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M. C. Thompson del.

THE AMERICAN SWALLOW BUG, *OECIACUS VICARIUS* HORVATH (HEMIPTERA, CIMICIDAE).

By L. EMERY MYERS.
Stanford University, California.

(With Plates X to XIII.)

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1. Introduction and acknowledgments.

Oeciacus vicarius Horvath is an ectoparasite of swallows in North America. It has at times been called the "barn swallow bug," but I have been able to find it in California only on the mud nests of the cliff swallow, *Petrochelidon lunifrons* (Say). As will be shown later, it appears that the term "barn swallow" has been carelessly used to include the cliff swallow as well, although it is possible that the bug occurs on more than one host species.

I first became interested in the swallow bug while banding a colony of cliff swallows that were nesting under the eaves of buildings on the Stanford University Campus. I have been banding swallows in this locality for the past three years and consequently have had an opportunity to observe the bugs over this period. The banding was done at night, as that is the most favourable time at which to find the birds in the nests. The habit of the bugs of feeding at night correlates very nicely with the habits of the hosts.

The cliff swallow frequently builds its mud nests under the eaves of houses and its parasite, the swallow bug, is occasionally seen by the occupants of the houses and considered to be the common bedbug. In many places it is an established belief that the swallows carry bedbugs. But in spite of this wide-spread knowledge of the occurrence of the insect there exists in the literature but little information concerning it. The original description of the species, occasional records of its occurrence and, here and there, a reference to the possibility that it may attack man, contribute practically all that is to be found.

In this paper I am presenting such information as I have been able to gather over a period of two years of observation.

Acknowledgments are due to Mr E. P. Van Duzee, Curator of Entomology, of the California Academy of Sciences, for the loan of material, representing several species of the family Cimicidae, which has been extremely useful for comparison. I wish also to thank Professor G. F. Ferris, of Stanford University, under whose direction this work has been done, for advice and for assistance in the preparation of this paper[1].

2. Review of the literature.

1890. *Abcanthia pipistrella* (sic), Gillette, *Entomol. News*, **1**, 26–27.
1892. *Cimex hirundinis* Jenyns, Osborn, *Canadian Entomol.* **24**, 264.
1895. *Acanthia hirundinis* (L.) (sic), Gillette and Baker, *Hemiptera of Colorado*, 56.
1896. *Acanthia hirundinis* (Jenyns), Lugger, *Ann. Report Div. Entomol. Minnesota*, **2**, 199–200.
1896. *Acanthia hirundinis* (Jenyns), Osborn, *U.S. Dept. Agric., Div. Entomology, Bull.* (n.s.), **5**, 161–162.
1900. *Acanthia hirundinis* (Jenyns), Lugger, *Ann. Report Div. Entomol. Minnesota*, **6**, 52.
1904. *Acanthia hirundinis* (Jenyns), Kellogg, *American Insects*, 206.
1912. *Oeciacus vicarius* Horvath, *Ann. Mus. Nat. Hung.* **10**, 216.
1914. *Clinocoris hirundinis* (Jenyns), Parshley, *Psyche*, **24**, 143.

Apparently the first record of this species is that of Gillette (1890) who found specimens of a Cimicid on the mud nests of swallows under the eaves of a barn on the Iowa Agricultural College Campus. He stated that "the eaves were completely lined with their mud nests between the ends of the rafters" and that the bug resembled somewhat the human bedbug but was "much smaller, more hairy and having a grayish pilose appearance instead of the naked, brick-red appearance of the human bed-bug." "The outsides of the nests," he says, "were in many places gray in colour from the accumulation of their white eggshells." The identification of the species was accredited to W. H. Ashmead, who stated that he believed that in most cases where bedbugs were reported from swallows' nests in this country they represented this species and not the human bedbug. It may be assumed that these were of the species which is now called *Oeciacus vicarius*.

Osborn (1892) pointed out that Ashmead had apparently misidentified this species and expressed his belief that the species recorded by Gillette was really *Cimex hirundinis* Jenyns. According to his observations the insects were "very abundant after the swallows had left and specimens kept in a bottle corked with a rubber stopper were alive and active the following summer, so it would seem an easy matter for them to remain in the nests until the return of the swallows in the spring."

Gillette and Baker (1895) merely record the species as taken from swallows' nests at Dolores, Colorado, in June.

Lugger (1896) stated that bugs similar to bedbugs attack chickens, pigeons, swallows and bats. The bugs found on the nests of swallows oftentimes reach

[1] Acknowledgments are also due to Dr Karl Jordan, from whom specimens of the European swallow bug were received after Mr Myers had completed his work.—G. F. Ferris.

the inside of the houses against which the birds have built their nests. These bugs, he stated, resemble the human bedbug except that they are much smaller, darker and cannot exist for any length of time away from their proper hosts.

Osborn (1896) practically reprints his paper of 1892. He adds the information that the eggs are probably laid early in the summer, soon after the swallows arrive and that the young become at least partially grown before fall. He suggested the possibility that the bugs take other food than the blood of the swallows.

Lugger (1900) practically reprints his notes of 1895, with some additional information. He states that a species of bedbug found on a school building in western Minnesota "became annoying during winter, and especially near the warm steam pipes. Later they invaded all the rooms...annoying teachers and students in broad daylight."

Kellogg (1904) noted merely that a species of *Acanthia* attacks chickens, pigeons, swallows and bats and that "Lugger found this species, *A. hirundinis*, or another similar one, attacking in day time the pupils in a school in western Minnesota."

Horvath (1912) was the first to recognize the species from swallows' nests in North America as distinct from the *Cimex hirundinis* Jenyns of Europe.

Parshley (1914) merely records the species as taken from nests of swallows in New England.

3. Systematic position.

The bibliography cited above shows that for many years the bug found on swallows in North America was considered identical with that found on swallows in Europe and which is now called *Oeciacus hirundinis* (Jenyns). The European species is the type of the genus. The American form was described as *O. vicarius* by Horvath in 1912.

Specimens have been forwarded by us to Dr Karl Jordan of the Zoological Museum at Tring, England, and he informs us that they are indeed distinct from the European *hirundinis*[1]. We are accepting the species found on cliff swallows as *O. vicarius* Horvath, although we have not seen authoritatively determined specimens.

At one time all the bugs commonly known as "bedbugs" were placed under the genus *Cimex* or its synonyms. More recently this genus has been split into a number of genera which are arranged in several subfamilies of the Cimicidae. Jordan has referred *Oeciacus* to his subfamily Clinocorinae, or Cimicinae, as it would now be called in view of the fixation of the family name Cimicidae, in company with the genus *Cimex*.

This splitting, especially as seen in the recent work of List, seems to have been carried to an extreme degree. The differences given as separating some

[1] Specimens of *O. hirundinis* were received through the kindness of Dr Jordan after Mr Myers' work was finished. The two species are indeed quite distinct, the organ of Berlese being very different.—G. F. Ferris.

of these genera and subfamilies are based in part at least on characters that appear to be nothing more than specific, such as the types of hairs. In the figures which follow there will be shown hairs of the different types taken from a single species. It is not possible, however, to consider this matter in any detail here because of want of material representing a number of the genera required for comparative study.

However, on the basis of such material as is available, it appears that the genus *Oeciacus* may very well be recognized as distinct at least from *Cimex*.

4. Morphology of the species.

Methods of study.

It has been the custom of systematists working on the Cimicidae to depend largely upon pinned material. This method allows one to see only a few of the major structures on the outside of the body and consequently appears to be inadequate for the purposes of a proper study. In the preparation of this paper I have based my study and my drawings upon specimens that have been cleared (and in some cases stained) and mounted upon slides where the higher powers of the microscope may be used. For certain purposes living material has been employed in order to give a clearer understanding of the relationships of the various parts.

Scope of this discussion.

In this paper, I shall not discuss the major characters that are common to all of the Cimicidae and which are well enough known from various studies of the common bedbug, *Cimex lectularius* Linnaeus. I shall confine the discussion primarily to the more specific characters and present it as an aid in separating this species from others and as an indication of the specific characters to be found in the group.

The Adult.

Size and form.

The general shape of *Oeciacus vicarius* (Plate X, fig. 9) is similar to that of the common bedbug, *Cimex lectularius*, but the former is smaller and more hairy. The adult female, as mounted on the slide, averages about 5·2 mm. in length and the male about 5·12 mm. Unmounted specimens would be somewhat shorter. The male differs from the female in the somewhat more slender form and the more pointed apex of the abdomen.

Proboscis. Proboscis short, scarcely reaching to the fore coxae. Its tip (Plate X, fig. 7) is roughened and bears a number of very small setae, which are possibly used to break the skin surface and permit the entrance of the thread-like mouthparts. The beak is apparently three-segmented.

Antennae. Antennae (Plate X, fig. 2) four-segmented. The hairs on the fourth segment are simple setae of that type shown in Plate XIII, fig. 14; those on the third segment are slightly serrate at the tip as shown in Plate XIII,

fig. 17; those on the first and second segments are laterally serrate as shown in Plate XIII, fig. 18.

Legs. The tarsi (Plate X, fig. 6) are three-segmented and there are no pulvilli. The anterior tibiae bear at the apex and on the cephalic side (that is, with the legs stretched out at right angles to the longitudinal axis of the body) a distinct comb of small setae (Plate X, fig. 1). This comb is apparently used as an antenna cleaner and possibly also to clean the proboscis, as I have noticed the antenna held in such a position that it passed between the combs. The opposite side of the leg is shown in Plate X, fig. 5. It should be noted that there is borne on all the legs, at the apex of the tibia, also a distinct brush of fine setae, as is shown in these figures.

The apex of the tibia in the second and third pairs of legs differ from that of the first pair, although it is nearly the same for these two pairs. The comb and brush of the fore legs are entirely lacking. In Plate X, fig. 10, is shown the arrangement of the setae on the cephalic aspect and in Plate X, fig. 24, the arrangement on the caudal aspect. Some attention was given to these setae on the apex of the tibiae of the second and third legs, as they offer some possibilities for the study of variation in the species. In Plate X, figs. 11 to 17, are shown variations in the arrangement of the setae on the caudal aspect, and in Plate X, figs. 18 to 23, variations of the cephalic aspect. These variations were taken from a study of fifty or more legs. The most common arrangement for the cephalic aspect is that of fig. 18 and for the caudal aspect that of fig. 11. Evidently the separation of species should not be based upon these characters.

The vestiture of setae. This species is more or less characterised by its vestiture of setae, which in life give it a somewhat silky appearance. In fact various authors have at times used this character as a "key character" for the separation of the species from the common bedbug. It has even at times been referred to as the "hairy bedbug." The general distribution of the setae is clearly indicated in Plate X, fig. 9.

The bases of the hairs on both dorsal and ventral sides of the body—but not on the antennae or legs—in this species are set in conspicuously large sockets which are somewhat pit-like. In *Cimex lectularius* and *C. pilosellus*, the latter occurring on bats, the hairs on the dorsal side of the body only are thus set in pits (Plate X, fig. 3), while those on the ventral side are set in the normal, slightly elevated sockets of the type shown in Plate X, fig. 4.

The types of setae found on *Oeciacus vicarius* are shown in Plate XIII, figs. 14 to 19, and may be compared with the types found in *Cimex pilosellus*, which are shown in Plate XIII, figs. 8 to 13. The types vary in a single individual of *Oeciacus vicarius* from a small, slender, simple hair to a long, curved hair which is coarsely serrate on its convex side. Some of the hairs (Plate XIII, fig. 15) are short and more spine-like, others are slender and serrate only at the truncate tip (Plate XIII, fig. 17). The hairs on *Cimex pilosellus* vary from a small, simple hair to a large, heavy and flattened, curved hair which is

minutely serrate on the convex side (Plate XIII, fig. 12). Another type of hair found on this species (Plate XIII, fig. 13) is heavy, only slightly curved and serrate only at the tip.

The two extremes represented by figs. 12 and 13 are types that have been used in the past for the separation of certain of the so-called subfamilies of the Cimicidae. The differences between the types of hairs—that is, whether they are serrate on one side or only at the tip—appear to be more in the nature of specific characters. In *Cimex pilosellus* the laterally serrate type is dominant on the margins of the pronotum and the abdomen. In another and apparently undescribed species of *Cimex*, likewise occurring on bats, the hairs of the terminally serrate type are predominant in these regions. According to some authors, the species with the laterally serrate hairs would be placed even in a different subfamily from that in which the hairs are predominantly serrate at the tips. Nevertheless, in comparing the two species they seem to be only specifically distinct.

The distribution of the setae on *Oeciacus vicarius* is as follows. The simple, slender setae (Plate XIII, fig. 14) occur on the fourth antennal segment. Along the ventral side of the fore tibiae the setae are short and stout (Plate XIII, fig. 15). Those of the other legs are very similar to those on the fourth antennal segment but are appreciably stouter (Plate XIII, fig. 16). Those of the third antennal segment are slender and slightly serrate at the tip (Plate XIII, fig. 17). Those of the remaining antennal segment and of the dorsal and ventral sides of the body are of the slender, laterally serrate type shown in Plate XIII, fig. 18. Those of the margin of the pronotum and on the female genitalia are shorter and less definitely serrate (Plate XIII, fig. 18).

In *Cimex pilosellus* the hairs of the fourth antennal segment are small and slender as in *O. vicarius* (Plate XIII, fig. 8). Those of the ventral side of the tibiae are larger and stouter (Plate XIII, fig. 9). Those of the third antennal segment and of the ventral side of the body are slender and slightly serrate at the tip (Plate XIII, fig. 10). Those of the dorsal side of the body are stouter and slightly serrate laterally. Those of the margins of the abdomen and on the female genitalia include both the large, stout, minutely serrate setae of Plate XIII, fig. 12, and the large, stout, apically serrate setae of Plate XIII, fig. 13.

The distribution of the setae on both dorsal and ventral sides of the abdomen are as shown in Plate XIII, figs. 5 and 6 for *C. pilosellus* and figs. 7 and 20 for *Oeciacus vicarius*. The setae on the dorsal side of *O. vicarius*, near the lateral margins, are relatively few and are confined to about four rows, while in *Cimex pilosellus* they are more numerous and form five or more rows. The hairs on the ventral side of *C. pilosellus* (Plate XIII, fig. 6) are more numerous than in the same region on *O. vicarius* (Plate XIII, fig. 20). In both species the hairs on the ventral side are more scattered and less definitely arranged in rows than on the dorsal side.

The differences in the character of the sockets of the setae have already been discussed.

Sense pits. On the dorsal side of the abdomen, the hemelytra and the pronotum, there occur near the lateral margins small sense pits of the form shown in Plate X, fig. 8. The adult insects possess eight or nine of these pits near the lateral margin on each abdominal segment, two on the hemelytra and eight or nine on the pronotum. These pits seem to be characteristic of *Oeciacus vicarius*, as the species of *Cimex* and *Haematosiphon* that I have seen do not possess them.

Organ of Berlese. On the right-hand side of the fourth abdominal segment is the peculiar organ which is known as the "organ of Berlese" (Plate X, fig. 9). The detailed appearance of the chitinous portions of this organ is shown in Plate XIII, fig. 4. It will be noted that there is a distinct notch in the posterior epiphysis of the segment, this leading to a small hair-lined pouch.

Various writers dealing with the common bedbug have assumed that this organ is an organ of copulation, as sperm has been found in the pouch. None, however, have been able to observe the insects actually in copulation. I have been able to observe a pair that were thus in copulation and to study their behaviour under the binocular microscope. It was possible to see the male remove his penis from this organ of Berlese, and consequently its connection with copulation seems to be definitely established.

It might be worth while to consider the variation in the structure of the organ of Berlese in various species. The shape of the organ appears to be quite characteristic in each form. The variation of the organ among the different species is so marked that its shape alone would serve as a very good character upon which to base their separation.

In *Cimex pilosellus* (Plate XIII, fig. 1) this organ forms a very broad sinuation in the margin of the fourth segment and the pouch is very deep and narrow and is lined with fine hairs. In another species of *Cimex*, occurring on bats and apparently undescribed (Plate XIII, fig. 2), the notch is very shallow and there is apparently no pouch. In *Cimex lectularius* (Plate XIII, fig. 3) the notch is very small and the pouch very inconspicuous. The figures are all to the same scale.

Genitalia. The genitalia of the female (Plate XI, fig. 1) seem to be identical with those of *Cimex lectularius* and present no specific peculiarities. Those of the male (Plate XI, figs. 3 and 5) seem also to be structurally the same as in the common bedbug. These structures have been discussed in detail by other workers and need not be considered further here.

Thorax and scent organ. The shape and dimensions of the pronotum and the hemelytra have commonly been used for the separation of species in this family. In the species that I have seen the differences in these structures seem so slight as to be insignificant. I am presenting, however, a figure showing the general appearance of the dorsum of head and thorax (Plate XI, fig. 2).

The ventral side of the thorax is shown in Plate XI, fig. 4, primarily for the purpose of indicating the position of the scent organ. This organ forms a portion of the pleural region of the metathorax and is a conspicuous feature

in slide preparations. The details of its position and its appearance are shown in Plate XI, fig. 6. The outer surface of the organ is marked by a characteristic pattern, which is shown in Plate XI, fig. 7. The organ is bi-valved, with a long, slit-like opening through which the oily scent fluid is extruded.

The posterior margin of the mesothorax shows a small region which bears the same characteristic markings that adorn the scent organ, but apparently it does not constitute a scent organ.

Immature Stages.

In all, the insect passes through six stages, including the adult, and there are consequently five moults. The differences between the immature stages are only slight. The most conspicuous changes are the increase in the number of hairs upon the body and in size from stage to stage. There is also a change in general proportions, the legs and antennae of the earlier stages being disproportionately large.

The sense pits, to which attention has been called earlier, are entirely absent on the margin in the first stage. Beginning with the second stage the pits are found on each side of the abdominal segments and the pronotum. There is but one pit on each side of the two wing rudiments in all the immature stages. The number of pits on each abdominal segment increases with each stage until there are eight or nine on each and the three or four on each side of the pronotum have increased to eighteen or twenty.

The most definite character for the separation of the immature stages is to be found in a group of very small setae at the base of the coxae. The position of these setae is indicated in Plate XI, fig. 6 *x*. In the first stage (Plate XII, fig. 7) there are but three of these setae and in the second stage (Plate XII, fig. 6) the same number. These two stages may be separated, however, on the basis of other characters which will be pointed out later. In the third stage (Plate XII, fig. 5) there are four of these setae, in the fourth (Plate XII, fig. 4) there are five, in the fifth (Plate XII, fig. 3) six and in the sixth or adult (Plate XII, fig. 2) seven. Minute as this character is, it seems to be constant and definite, for it has held through a series of from ten to twenty specimens of each stage. It likewise holds in the immature stages of *Cimex lectularius*.

The first and second stages, which are the same in respect to these minute setae, may be separated by the arrangement of the sense pits on the abdominal segments, the first stage (Plate XII, fig. 10) having none near the lateral margins and the second (Plate XII, fig. 11) having two marginal pits on each segment.

The genitalia being entirely undeveloped in the immature stages, it is impossible to distinguish the sexes. In Plate XII, fig. 8, is shown the apex of the abdomen of the fifth stage.

In all the immature stages the tarsi (Plate XII, fig. 9) are but two-segmented, in contrast to the three-segmented tarsi of the adult.

In all the immature stages the first and second abdominal segments are entirely unchitinised and are almost transparent. This gives the immature

stages the appearance of having a white band separating the abdomen from the thorax.

In Plate XII, fig. 12, is shown the general form of the head, thorax and first two abdominal segments. In all the immature stages there is a curious condition of the wing rudiments. Although the hemelytra at maturity are entirely separate, there are at no time any separate wing pads. The posterior margin of the notum of the mesothorax is continuous, but even in the first stage forms a free epiphysis. And, although the posterior wings are never developed, the same condition is found on the notum of the metathorax. The posterior portions of both of these segments can be lifted up and be seen to be entirely free. In view of the very small size of the wing vestiges in the adult, it is possible that actually no wing pads are developed.

The average lengths of the various immature stages is as follows: first stage 1·12 mm., second stage 1·76, third stage 2·48, fourth stage 2·88, fifth stage 3·92. These are measurements of specimens as mounted on slides and consequently they are probably somewhat longer than measurements taken from living or dried specimens would be. There is some overlapping of the various stages and the above measurements are only averages.

5. Biology.

Hosts.

In the locality in which this work has been done, *Oeciacus vicarius* seems to occur only in the mud nests of the cliff swallow, *Petrochelidon lunifrons* (Say). It is possible that the species may occur on other swallows but I have been unable to find any Cimicids in the nests of the barn swallow, *Hirundo erythrogaster* Bodd.

Oeciacus vicarius has commonly been called the "barn swallow bug," but it appears that the term "barn swallow" has been used carelessly to apply to the cliff swallow. At least in each of the cases of records of this bug where any information concerning the hosts is given the description of the nests applies to those of the cliff swallow and not to those of the barn swallow. It is possible that the species is confined strictly to the cliff swallow and it might properly be called the "cliff swallow bug."

In connection with the subject of hosts, it is of interest to consider the possibility that the species may feed upon man. The occurrence of the nests of its host about the dwellings of man and the appearance of enormous numbers of the bug frequently leads to questions concerning this possibility.

In looking through the literature concerning this species, I have found no positive record of their attacking man[1]. Lugger, in his report of 1900, stated that during the winter they annoyed teachers and students in a school, although he does not specifically state that the persons were actually bitten. I first discovered that they will feed quite readily on man when I found small

[1] Professor Ferris informs me that he is sure there has been such a record within recent years, but he cannot recall the place of its publication and I have not been able to trace it.

welts appearing on my arms about the second day after I had begun banding swallows. Then one evening I found an immature bug actually feeding on my arm. I therefore tried several experiments with feeding the bugs upon myself. The details of these experiments will be found in the later discussion of the biology of the insects, and it is sufficient to say at this point that there is no question of the ability of the bug to feed upon man and to grow and produce eggs on a diet of human blood.

Nevertheless, it appears that under normal conditions the insects will not readily transfer to man, for although I have banded swallows through three seasons and have frequently found the insects in my clothing they have never established themselves in my room.

Life-history.

This account of the life-history of the swallow bug is to a certain extent incomplete owing to difficulties that arise in dealing with its host, since it is impracticable to keep swallows in captivity. I have been able to make certain observations of the insects in the nests of their hosts, but a large part of my data have been taken from specimens that were kept in captivity and fed upon myself. The lengths of the egg stage and the various instars were thus secured.

The cliff swallows appear at Stanford in the latter part of March and take up their abode in the old nests remaining from the years before. A small number of the bugs have hibernated in the cracks of the old nests and they soon come out to feed upon the swallows. A mud nest taken down on February 23, 1927, before the swallows arrived, had about a hundred living bugs in various stages from the second instar to adults.

There is a possibility that small numbers of the bugs are taken south with the swallows in the fall and return with them in the spring. In this way new colonies of the birds might become infested. A small example which illustrates the possibility of their transportation in this way was seen. In the spring of 1926 the swallows returned to the nests built in 1925, which were infested with bugs that had hibernated. A couple of weeks later many of the birds were frightened away and built new nests in another location at some distance away and where there had previously been no nests. Of these new nests a large majority were free from the bugs, while a small proportion showed several bugs present by the time they were completed.

In a very short article dealing with the swallow bug of Europe (*Oeciacus hirundinis*), it has been stated that bugs fed upon human blood will not lay eggs. It should be noted that in this case the experiment was continued only through a period of two weeks. In my experiments the bugs that were taken from hibernation on February 23, 1927, and fed upon myself until June, 1927, laid no eggs although they were seen to copulate. Other bugs that were taken April 7, 1927, after they had fed upon swallows, were paired off and those that were then fed upon myself laid eggs from April 29 to May 19 and these eggs hatched in from twelve to sixteen days. Those which were not fed upon

myself after being taken from the swallows on the same date laid eggs between April 22 and May 3 and the eggs hatched in from fourteen to twenty days.

Eggs laid on the nests were noticed at about the same time when eggs were laid in captivity and the periods of incubation were about the same. The previous year the first eggs were noticed on the nests on April 28. The majority of the eggs are deposited on the outside of the nest, several inches from the nest opening. On removing a nest only a small number of the eggs were found inside.

The eggs laid in capitivity on April 22, 1927, began to hatch on May 5, the period of incubation being thus fourteen days. The eggs in the nests were noticed to be hatching at the same time. The records taken from eggs laid in captivity in 1927 showed that the period of incubation varied from twelve to twenty days. Eggs laid by the same female on the same day showed a variation of as much as four days in hatching. Certain eggs laid on June 5, 1926, hatched in from eight to nine days. It is probable that this acceleration was due to the increased temperature in June.

On June 13, 1926, fifteen bugs were placed in a bottle having a cotton stopper. Eggs were deposited on June 5 and 6. The adult bugs were not fed. Thirteen died before the end of July, one lived until November 15 and the last died in the latter part of December. The eggs deposited on June 5 and 6 were placed in separate bottles. They hatched between the 13th and the 15th. The young would not feed the first day but fed readily the second day. I was able to raise one to the fifth stage by feeding it upon myself but it finally died in the latter part of December. It thus lived for nearly six months on human blood. It was fed about once a week until October 29 but from then on it would not feed. The three moults which took place occurred at ten-day intervals, the first on July 4, the second on July 14 and the third on July 25.

This is the only information available concerning the duration of the instars and it is probable that this is affected by the nature of the food.

Although no exact information concerning the rate of development is available, it is evident that this is rather rapid. A swallow nest was taken down on June 4, 1926—*i.e.* barely over two months after the first eggs were noted—and at this time 1333 bugs, ranging from the second instar to adults, were found upon it. While large numbers of the first instar were present, it was impractical to try to count them, so it is evident that there were probably not less than fifteen hundred individuals on the nest. It is evident, then, that the rate of development is quite rapid. By the end of the summer the nests are literally swarming with the bugs and the outsides are gray with the egg shells.

No information is available as to the effect of the bugs' feeding upon the birds, although it might be expected that the continued feeding of such enormous numbers of the insects upon the two adults and maximum of four young would be extremely harmful. I have on several occasions found dead

birds in the nests, both adults and young, and it is conceivable that their deaths might have resulted from the attacks of the insects. It is evident, however, that the birds must have developed a surprising degree of immunity to the attacks of the bugs. If one reflects upon the effect which would be experienced by a man endeavouring to sleep for even a single night in a bed infested by fifteen hundred bedbugs, one's sympathies for the birds cannot but be aroused. I have no information as to how frequently the individual bugs feed upon the birds, but I have been unable to induce them to feed upon myself more often than once in every four or five days and in my experiments I made a practice of feeding them not more often than once a week.

The feeding is painless—at least in my own experience—and only in a few cases is there the slightest sensation as the mouthparts are forced through the skin. The time of feeding varies from one to four minutes, three minutes being the average for the immature stages, while one and a half to two minutes is about the average for the adults. In one case, an adult female remained with the beak inserted into the skin for twelve minutes although for only a portion of this time was blood being drawn into the body.

If a bug is not disturbed after placing it on the skin, it will often clean its rostrum and antennae with the two fore legs both before and after feeding. In feeding the rostrum is placed against the skin in an extended, vertical position. The bug remains motionless for from thirty to fifty seconds and then the head is bent down three or four times, each time forcing the mouthparts downward. This apparently drives the mandibles and maxillae into the skin. Sometimes the head is bent down during feeding and at other times it is drawn back, stretching the rostrum to its full length. The first and second immature stages will often increase in volume as much as three times during feeding. The adults with a full feeding never increase more than twice in size and usually not so much.

Normally the bugs feed at night, as an examination of the nests at that time will show large numbers of the bugs moving about and gorged with blood. During the day they hide away in cracks in the nest. Nevertheless, bugs in captivity will feed in the daytime as readily as at night.

The effect of the feeding is to produce a slight pink discoloration some ten to twenty hours afterwards. Thirty to forty hours later a slight bump will appear and this will itch quite severely if it is scratched. It is often possible to squeeze a watery liquid from the welt. With the bugs which hatched in June, 1926, and which were fed only upon myself only a slight discoloration appeared after the first feeding. From then on they produced no visible effect. The characteristic welts appeared after feeding the bugs taken from hibernation in February, 1927, these not having been fed upon swallows since early fall.

A characteristic odour is given off by the insects upon the slightest irritation. It arises from the scent organs which have already been described. The first, second and third immature stages have the glands present but the odour

is apparently lacking in these stages. The fourth and fifth stages give off a slight odour when first irritated.

The swallow bug has several enemies. I have seen the swallows, while sitting at the openings of their nests, pick at the bugs that lined the openings. However, the birds did not appear to be eating the bugs. The swallow, being exclusively insectivorous, might be expected to feed upon these bugs, but I suspect that the odour given off protects them.

Apparently, the most important enemies of the bugs are spiders that attach their webs to the swallows' nests. It is a common occurrence to see the webs filled with the skins of the bugs upon which the spiders have fed. A reasonable estimate of the number of skins in some of the nests would be from 1500 to 2000. One of the common spiders about the nests is the "black widow," *Latrodectes mactans*, and the skins are to be found in its nest, as well as in the webs of other species. I have seen the bugs actually being eaten by the spiders. It is possible that after the birds leave in the fall these spiders greatly reduce the numbers of the hibernating bugs.

6. SUMMARY.

The swallow bug, *Oeciacus vicarius* Horvath, is of common occurrence in North America, chiefly, if not entirely, upon the cliff swallows, *Petrochelidon lunifrons* (Say); it has been recorded from the barn swallow, probably in error.

It appears to be really distinct from the European swallow bug, *Oeciacus hirundinis* (Linnaeus).

The habits, structure, and specific characters of the bug do not seem to have been adequately studied hitherto.

This paper deals with the external structure of the bug and of such of its biology as could be worked out under the handicap that its natural host could not be kept in captivity.

The bugs attack man readily, but do not appear to adapt themselves readily to living upon man or in his dwellings.

EXPLANATION OF PLATES X—XIII.

PLATE X.

Oeciacus vicarius Horvath.

Fig. 1. Cephalic aspect of apex of fore tibia of adult.
Fig. 2. Antenna of adult.
Figs. 3 and 4. Bases of setae.
Fig. 5. Caudal aspect of apex of fore tibia of adult.
Fig. 6. Tarsus of adult.
Fig. 7. Apex of rostrum.
Fig. 8. Sense pit.
Fig. 9. Adult female.
Fig. 10. Cephalic aspect of apex of tibia of either second or third leg.
Figs. 11–17. Variations in setae on caudal aspect of apex of tibia of either second or third leg.

Figs. 18–23. Variations in setae on cephalic aspect of apex of tibia of either second or third leg.
Fig. 24. Caudal aspect of apex of tibia of either second or third leg.

Cimex pilosellus (Horvath).

Fig. 4. Base of seta from ventral side of abdomen.

PLATE XI.

Oeciacus vicarius Horvath.

Fig. 1. Genitalia of adult female.
Fig. 2. Dorsal aspect of head and thorax of adult.
Fig. 3. Genitalia of male, dorsal aspect.
Fig. 4. Ventral aspect of thorax and first abdominal segment of adult.
Fig. 5. Genitalia of male, ventral aspect.
Fig. 6. Portion of ventral aspect of thorax, showing position of scent organ.
Fig. 7. Portion of ornamentation of scent organ.

PLATE XII.

Oeciacus vicarius Horvath.

Fig. 1. First stage.
Fig. 2. Seta cluster on coxa of adult.
Fig. 3. „ „ fifth stage.
Fig. 4. „ „ fourth stage.
Fig. 5. „ „ third stage.
Fig. 6. „ „ second stage.
Fig. 7. „ „ first stage.
Fig. 8. Apex of abdomen of fifth stage, ventral aspect.
Fig. 9. Tarsus of fifth stage.
Fig. 10. Dorsal aspect of margin of abdominal segment of first stage.
Fig. 11. „ „ second stage.
Fig. 12. Dorsal aspect of anterior portion of body of fifth stage.

PLATE XIII.

Oeciacus vicarius Horvath.

Fig. 4. Organ of Berlese.
Fig. 7. Dorsal aspect of margin of abdominal segment.
Figs. 14–19. Types of setae.
Fig. 20. Ventral side of margin of abdominal segment.

Cimex pilosellus Horvath.

Fig. 1. Organ of Berlese.
Figs. 8–13. Types of setae.

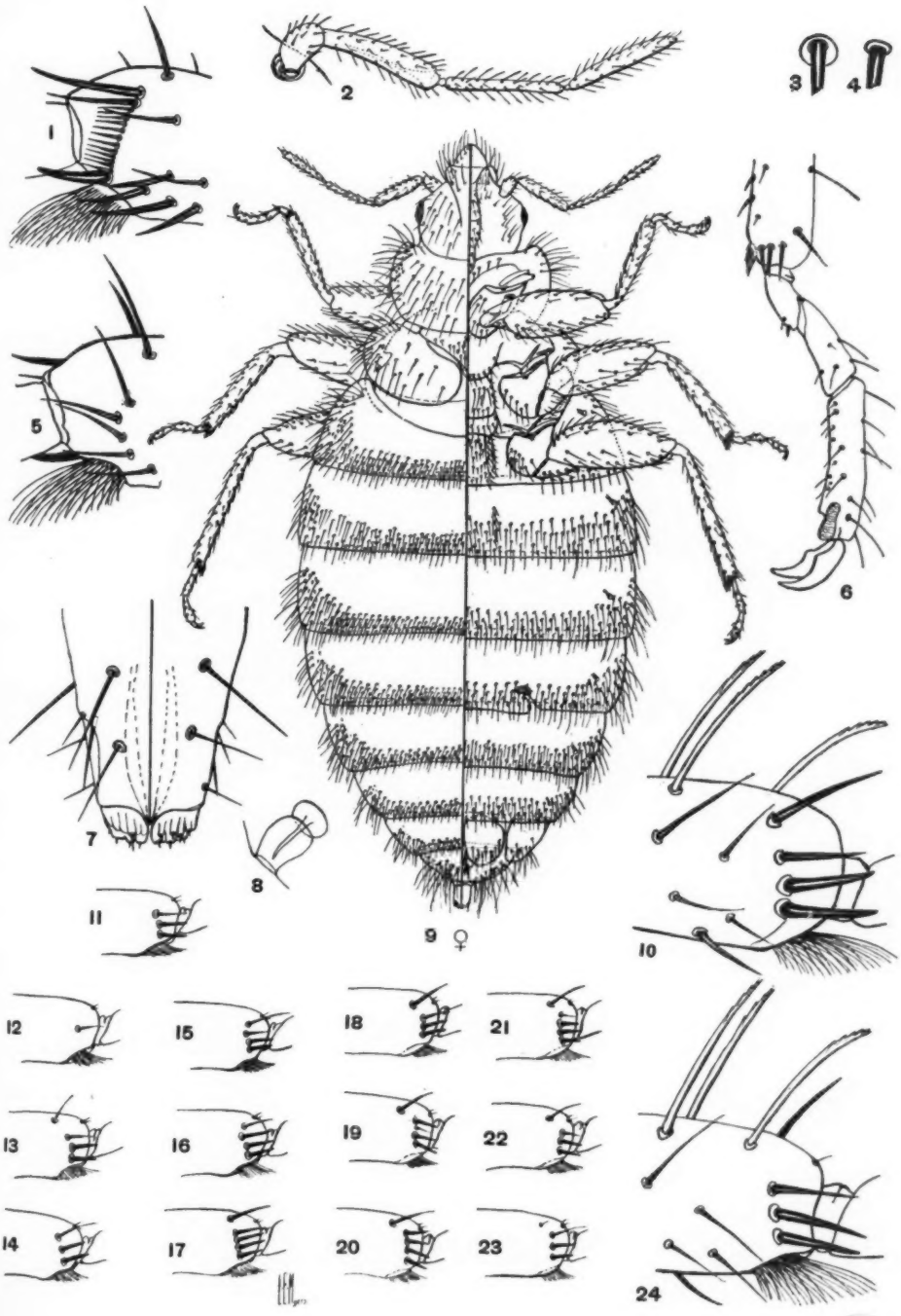
Cimex sp.

Fig. 2. Organ of Berlese.
Fig. 5. Dorsal aspect of margin of abdominal segment.
Fig. 6. Ventral aspect of margin of abdominal segment.

Cimex lectularius (Lin.)

Fig. 3. Organ of Berlese.

(*MS. received for publication* 2. II. 1928.—Ed.)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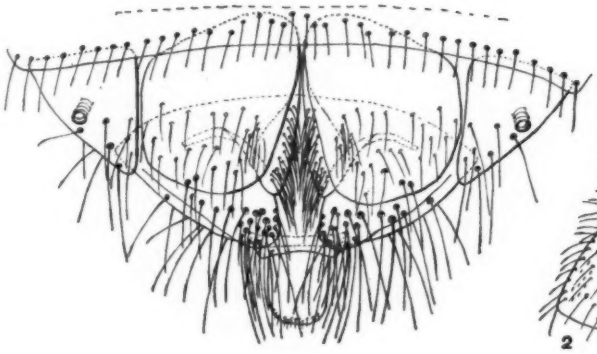

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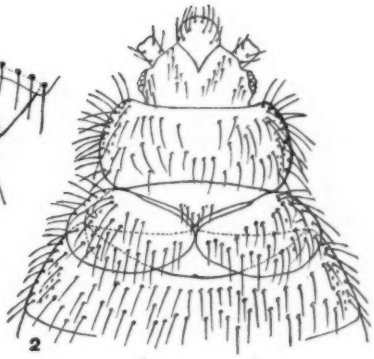

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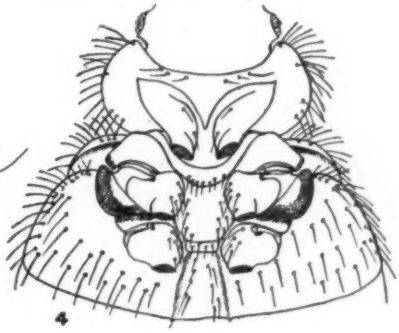

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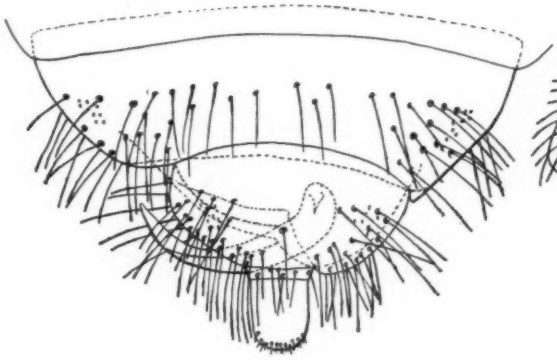

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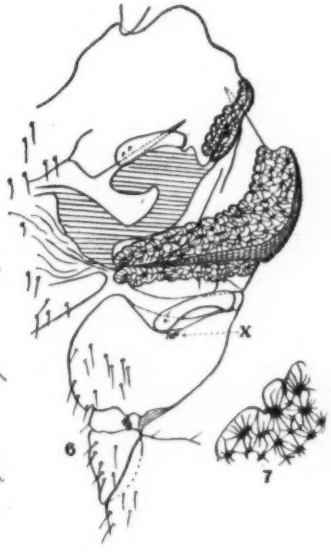

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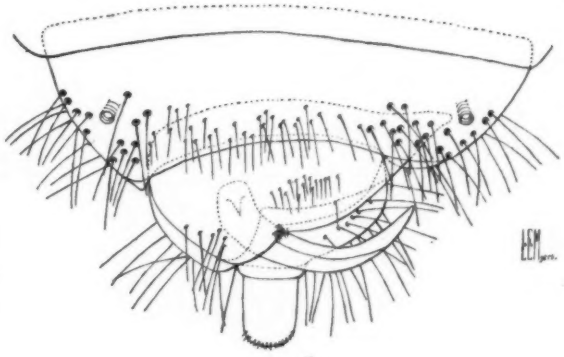

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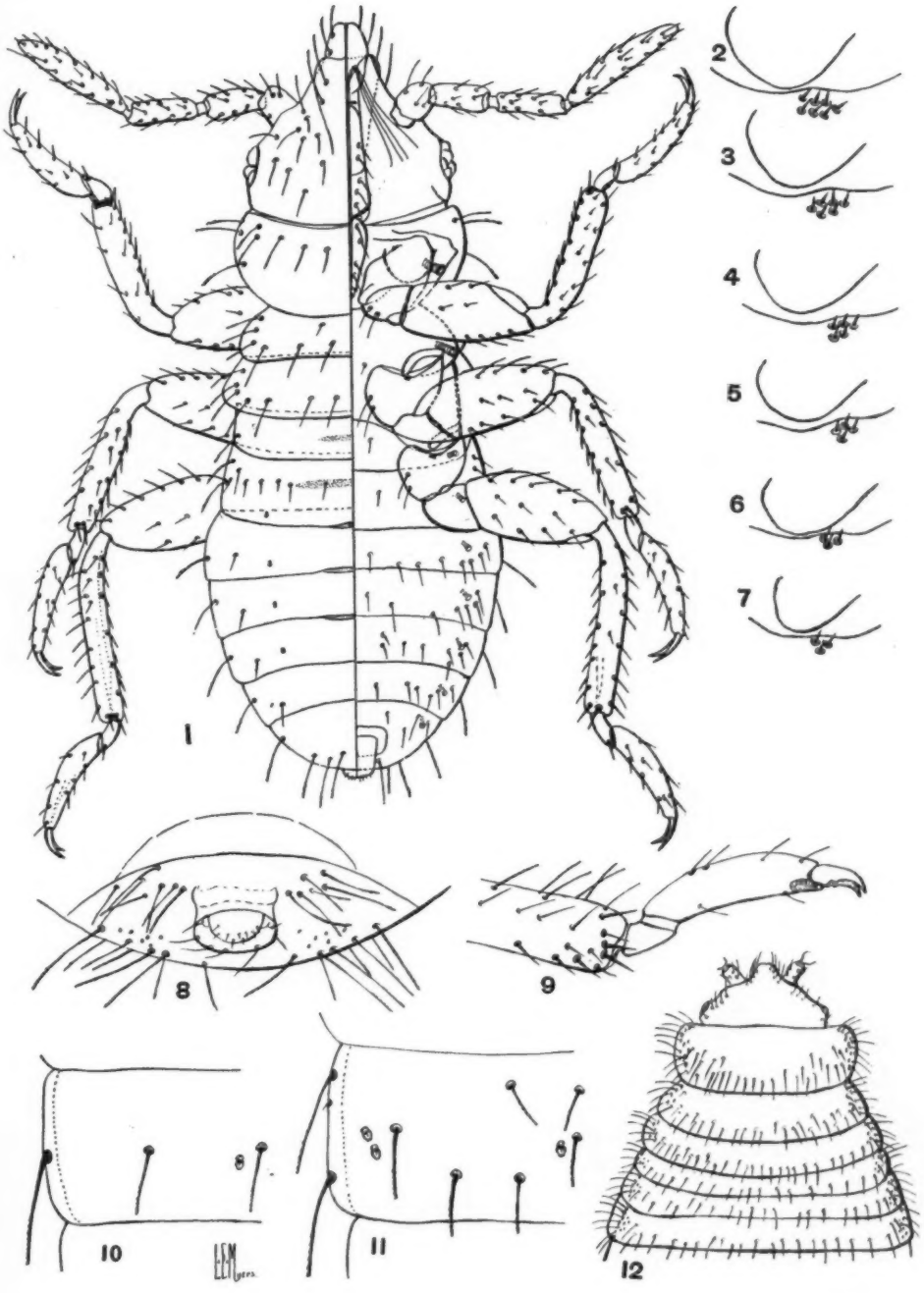
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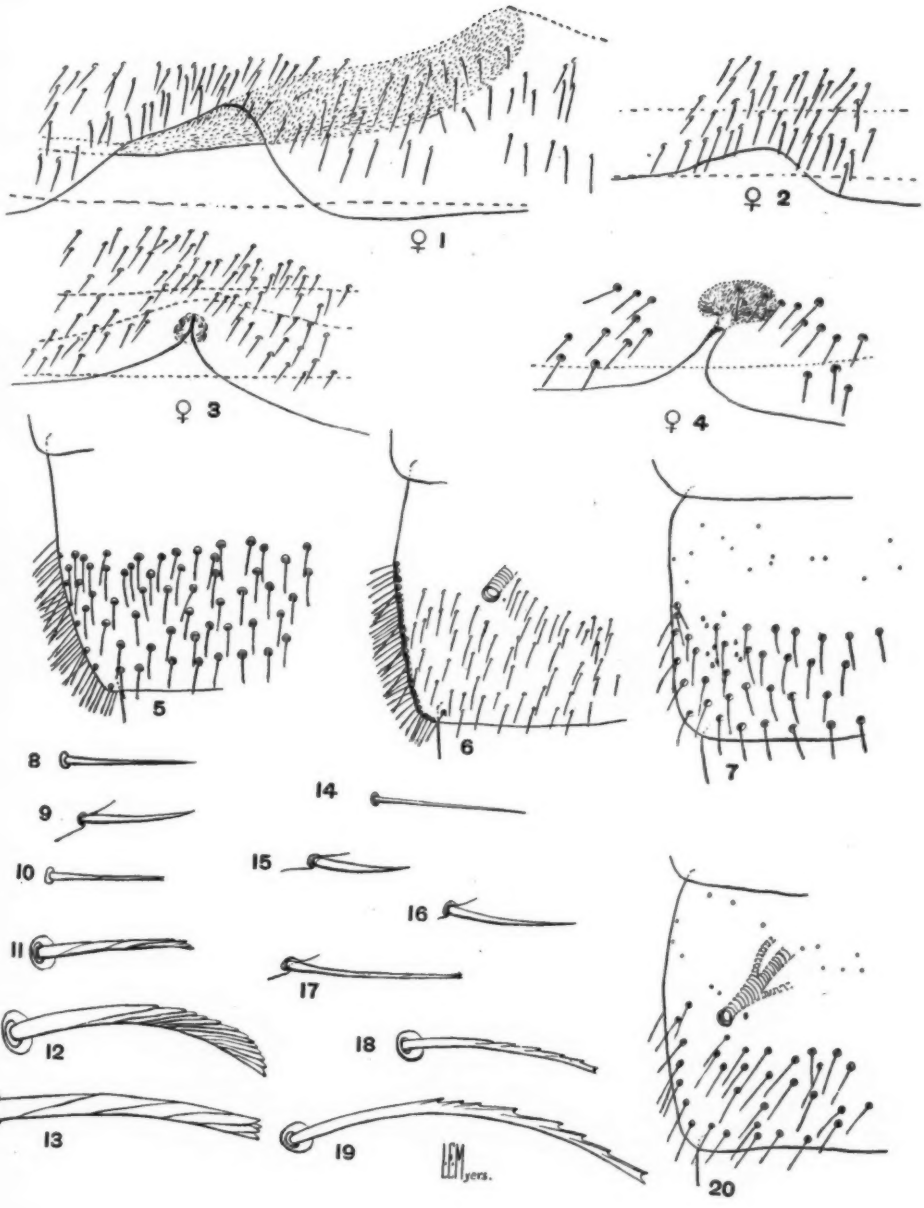

UNIV OF MICH.

NOTES ON A SMALL COLLECTION OF BAT ECTO-PARASITES.

By ROBERT MATHESON.

Department of Entomology, Cornell University.

During the summer of 1927 Mr W. J. Hamilton, a student in the Department of Entomology, Cornell University, collected biological material in parts of Cuba, Panama, and Costa Rica. He brought two small vials of parasites taken from bats. Though the collection contained only 24 specimens yet it is of interest on account of the rarity of some of the species. It is, therefore, thought worth while to offer the following brief notes on the species taken.

Spelaeorhynchidae (Acarina).

Neumann (1902) described *Spelaeorhynchus praecursor*, n.g., n.sp. from four specimens found in a vial in the Berlin Museum. The vial contained the tick, *Hyalomma aegyptium*, but the country of origin was not indicated. As the tick, *H. aegyptium*, is African and one of its hosts the ox, Neumann thought the four associated specimens probably came from that country and from the same host. Later (1905) Neumann found a single mutilated specimen in the British Museum, labelled "From *Carollia brevicauda*. Pernambuco. J. F. G. Smith." He then states that the association of this species with the African tick was due, in all probability, to an error in handling material. He now gives the country of origin as tropical America; host, bats.

Oudemans (1902) places *S. praecursor* Neumann in a separate family *Spelaeorhynchidae*, intermediate in some respects between the Parasitoidea and the Ixodoidea. Neumann (1911) places the species in a sub-family, *Spelaeorhynchinae*, of the Ixodidae. Banks (1915) accepts Oudemans' classification and places it as a family in the Parasitoidea.

Banks (1917) describes a new species, *S. latus*, from bats taken at Obispo, Canal Zone. During the summer of 1927 Mr W. J. Hamilton collected 12 ♀♀ of *S. latus* Banks from a species of bat (*Artibeus jamaicensis parvipes*) taken at Los Angeles, Oriente Prov., Cuba. It would seem remarkable that this peculiar family should be confined to the new world and be represented by only two species. The differences between the two species are very slight and *latus* Banks may yet prove a synonym of *praecursor* Neumann. It is hoped that collectors of bats will search more diligently for specimens of this peculiar family of mites.

Polyctenidae (Hemiptera).

The species of this family are all parasitic on bats. At the present time the family contains five genera and 13 species, represented in the collections of the world by 24 males, 34 females (one male and one nymph, types of *Polyctenes molossus* Gigl., lost). The genera, the number of species and the number of specimens representing them are as follows: *Androctenes* (1, 1 ♀, African), *Eoctenes* (3, 7 ♂♂, 12 ♀♀, 6 nymphs), *Hesperoctenes* (7, 15 ♂♂, 18 ♀♀, 8 nymphs, 3 larvae), *Hypoctenes* (1, 1 ♂ and 1 ♀, African), *Polyctenes* (1 ♂, 2 ♀♀, 1 nymph). The American species constitute the genus *Hesperoctenes*, of which there are seven. Of these only two species are represented by specimens in American collections—*H. longiceps* by 2 ♂♂, 3 ♀♀, 2 nymphs, 1 larva in the collections of Stanford University; 1 ♂, 1 ♀, 5 nymphs in the collection of Costa Lima; *H. tarsalis* by 1 ♂ in the collection of Cornell University[1].

The single male of *H. tarsalis* was taken by W. J. Hamilton on bats (*Tadarina*, sp. probably *mexicana*) at Turrialba, Costa Rica, at an elevation of 2500 ft. on 7. VIII. 1927. As this genus seems to be peculiar to the Americas it is hoped that collectors of bats will exercise every care in searching for external parasites and send them to our Museums.

Streblidae (Diptera, Pupipara).

Trichobius dugesii Townsend.

Seven females and two males were taken from bats (*Artibeus jamaicensis parvipes*) at Los Angeles, Oriente Prov., Cuba, on 28. VI. 1927.

Pterellipsis aranea Coq.[2]

One male from a bat (*Artibeus jamaicensis parvipes*) taken at Los Angeles, Oriente Prov., Cuba, on 28. VI. 1927.

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[1] I am informed that there are specimens in the U.S. Nat. Coll. but have been unable to obtain any details about them.

[2] The figure of the wing of this species by Kessel (1925) is in error. On the median vein there are three spines beyond the cross-vein and one in front of it. Kessel's figure corresponds to that given by Speiser (1900) for his *Megistopoda desiderata* which he later considered a synonym of *P. aranea* Coq. I have examined Coquillett's types and the specimen from which Kessel secured her figure and they agree with my interpretation. If Speiser's figure is correct it may be that *desiderata* should be considered a distinct species.

(*MS. received for publication* 7. II. 1928.—Ed.)

ORNITHOMYIA AVICULARIA (DIPTERA HIPPOBOSCIDAE) AS THE CARRIER OF MALLOPHAGA, WITH SOME REMARKS ON PHORESY IN INSECTS.

By CECIL WARBURTON, M.A.

From the Molteno Institute for Research in Parasitology, University of Cambridge.

(With 1 Figure.)

In July, 1927, Dr Kenneth Smith took a specimen of the Hippoboscid fly *Ornithomyia avicularia* on the window of a building at the Cambridge University farm. The fly was lethargic and easily captured, and, noticing that its abdomen was infested by some parasite, the captor kindly handed me the specimen.

Firmly attached by their mouth parts to the hairs of the abdomen I found no fewer than twelve adult bird-lice (Mallophaga) which Mr James Waterston of the British Museum has kindly identified as *Degeeriella marginalis* Nitzsch in Burmeister, a form usually found on the genus *Turdus*, and rendering it probable that the fly had recently infested a blackbird, *Turdus merula*.

In October, 1890, the late Dr David Sharp exhibited before the London Entomological Society an example of the same fly, taken near Dartford, "to which there were adhering—apparently by their mandibles—several specimens of a Mallophagan insect." The Mallophagan was not identified, and no comments on the exhibit were recorded, but from the fact that in Dr Sharp's account of the Mallophaga in Vol. v of the *Cambridge Natural History*, published in 1910, allusion is made to this case alone, it would appear that the observation was a new one and remained to that date unique.

About this time, however, I find three records of similar phenomena. In 1910 Mjöberg, in his "Studien über Mallophagen und Anopluren," states that he caught two specimens of *Ornithomyia*, not long from their hosts, one with seven and the other with three specimens of *Docophorus leontodon* firmly attached; and Prof. B. Warnach of Potsdam gives a lively account of an incident which befell him on a country walk. His attention was attracted by sounds of distress uttered by a blackbird, which was behaving in a very odd manner, with its neck twisted and its head bent down on the breast. Unable to afford it any relief, he killed it to end its sufferings, and took it home to examine it for parasites. On opening the bag, three specimens of *O. avicularia* flew out, and on the abdomen of one he found a *Philopterus* sp. He

remarks that it is unlikely that such "a specialist in birds' feathers" should derive any satisfaction from the slender hairs of a fly, and that its object is no doubt the finding of a new host. A search among the feathers of the bird did not reveal the presence of any further examples of the Mallophagan, the species of which is not named.

Then in 1911, E. Jacobson states that three years previously he shot, near Batavia, a bird, *Eucichla cyanura*, from which a fly, *Ornithoeca pusilla*, escaped, bearing—"clasped between its legs"—a Mallophagan, unidentified, —an account which would rather indicate that the carriage was deliberate on the part of the fly!

The carriage of *Pediculus* on house-flies has been observed occasionally. Nuttall (1918), in a "Note on Lice and Flies" in his "Biology of *Pediculus humanus*," quotes S. Calandruccio (1890), as stating that he has seen *Pediculus* conveyed by flies, and also Bohne, who in 1915 published a paper entitled "Stubenfliegen als Träger von Läusen." These cases are not quite on the same plane as the foregoing since, while a bird-louse on *Ornithomyia* is fairly certain to be carried to its appropriate host, *Pediculus*, mounting a house-fly, is trusting very much more to chance. It is very unlikely to be conveyed directly to its host, though there are fair prospects of its reaching a human habitation.

In 1896, P. Lesne proposed the name *Phorésie* for the phenomenon of the deliberate utilisation of another creature for conveyance only, and, anglicised as Phoresy—Phoresis would perhaps have been preferable—it has been adopted by several writers, new instances being frequently cited.

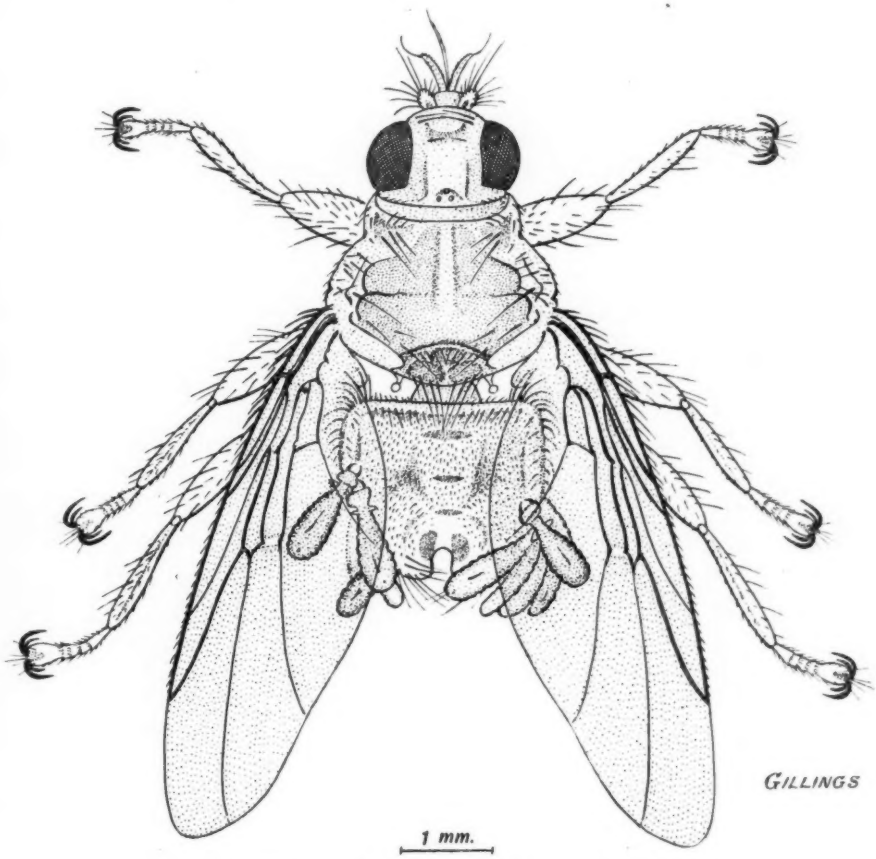
Lesne's typical example was the Borborid fly *Limosina sacra*, which he constantly found riding on a dung-beetle, *Ateuchus laticollis*, in Algeria, apparently for the purpose of ovipositing in the particularly choice assemblage of faecal matter which the beetle had been at the trouble of collecting and consolidating. Though perfectly well able to fly, the *Limosina* preferred this method of attaining its object, and refused to be dislodged by any antics of the beetle, though it readily evaded capture on its own account by flight. This was, of course, no new observation, for the fly was originally named by Meigen (1838) from its occurrence on *Ateuchus sacer*, and several authors had since noted its presence on that beetle.

In 1926, Dr Ferrière of Berne reviewed the whole subject of Phoresy. He recognised the difficulty of deciding in some cases whether their inclusion under the title is justified, for, on the one hand, accidental transportation must be excluded and on the other, there must be no parasitism on the vector. It is probable that alleged cases of Phoresy on the part of Chironomid flies are really cases of parasitism. It is clear, as Dr Ferrière remarks, that the deliberate selection of a vector by an adult Ichneumonid must be true Phoresy.

Dr Ferrière instances about fifteen cases of undoubted Phoresy, and there is no doubt that the list might be very greatly extended.

Even so limited, it is obvious that there are two categories into which examples of this phenomenon may fall. There are the cases of simple migration,

where the attainment of no particular host or specially favourable locality may be depended on, and there are the cases where there is every prospect of conveyance to the precise spot desired. The latter class, into which falls the instance here recorded, contains the cases of greatest interest. None, perhaps, is more remarkable than that of the Scelionid *Rielia manticida*, parasitic on the eggs of a Mantis, described by L. Chopart. Its ovipositor is



Ornithomyia avicularia carrying *Degeeriella marginalis*.

feeble and cannot pierce the hardened cement enveloping the eggs of the Mantis, so that it is necessary for it to be at hand at the moment of oviposition. It, therefore, remains attached to the body of the Mantis—sometimes for months—and oviposits in the eggs as they are extruded, half drowned in the still liquid cement. Another egg parasite of the Mantis, *Podagrion pachymerum*, possessed of a more powerful ovipositor, has no such habit.

I am greatly indebted to Mr James Waterston of the British Museum of Natural History, who identified the Mallophagan carried by *O. avicularia* and assisted me in looking up the literature of the subject.

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(*MS. received for publication* 15. II. 1928.—Ed.)

THE GENERA *SPHYRION* AND *BASANISTES* (COPEPODA) AS REPRESENTED BY THE COLLECTION IN THE BRITISH MUSEUM.

By W. HAROLD LEIGH-SHARPE, M.Sc. (Lond.)

Lecturer in Zoology, Chelsea Polytechnic, London, S.W. 3.

(With 4 Text-figures.)

Family Sphyriidae Wilson (1919).

Genus **Sphyrion** Cuvier (1830).

Generic Diagnosis, ♀. *Cephalothorax* with transverse lateral expansions, small in young, resembling a hammer in old specimens, between whose anterior surfaces projects the head. *Neck* smooth, cylindrical and without swimming feet. *Trunk* much enlarged transversely, smooth, flattened dorsiventrally, bearing a pair of posterior appendages profusely and dichotomously branched. *Abdominal appendages* reduced to two small knobs; or one undivided abdomen. *Egg-strings* long and straight; eggs multiseriate. Two pairs of antennae, two pairs of maxillae, one pair of maxillipedes.

The biconvexity or biconcavity of the trunk is of no importance in determining species. Thus in *S. lumpi* (*vide infra*) the specimen (*a*) is plump, pale chrome yellow, with trunk strongly biconvex, while (*b*) has a desiccated brittle appearance, is dark brown, very translucent, with trunk markedly biconcave.

S. lumpi (Krøyer 1845).

Material. (*a*) 1 ♀ (1913.9.18.327)[1] from *Anarrhichas lupus* in the North Sea, presented by T. Scott (Fig. 1, *A* and *B*). *Dimensions*: length of head and neck 21 mm. Lateral expansions: width 8·5 mm. Length of trunk 11 mm., width 12 mm., posterior processes 7 mm., abdominal bifurcations 2·1 mm. Total length 35·1 mm.

(*b*) 1 ♀ (1911.11.8.47824) an older specimen, labelled from Iceland (outer label), and, probably more correctly, from Greenland (inner label). Copenhagen Mus. Norman Coll. (Fig. 1, *C*).

Diagnosis. *Cephalothorax* enlarged by lateral expansions until it is three-quarters the width of the trunk in the young specimens usually described, but considerably wider in older specimens with a tendency to bifurcate at the lateral apices. *Neck* much longer than trunk, fully as long in young specimens

[1] The numbers cited after the specimens refer to the Register in the British Museum, Crustacea Department.

as in older ones. *Trunk* obcordate, strongly flattened dorsiventrally, width and length approximately equal, a trifle wider than long, lateral margins rounded, posterior margins straight. Posterior processes, stout, more than half the length of the trunk in young specimens and becoming more profusely branched as the animal matures. *Abdomen* small, bilobed at the posterior end; abdominal appendages reduced to two small knobs on the ventral aspect. *Egg-strings* lacking in both specimens.

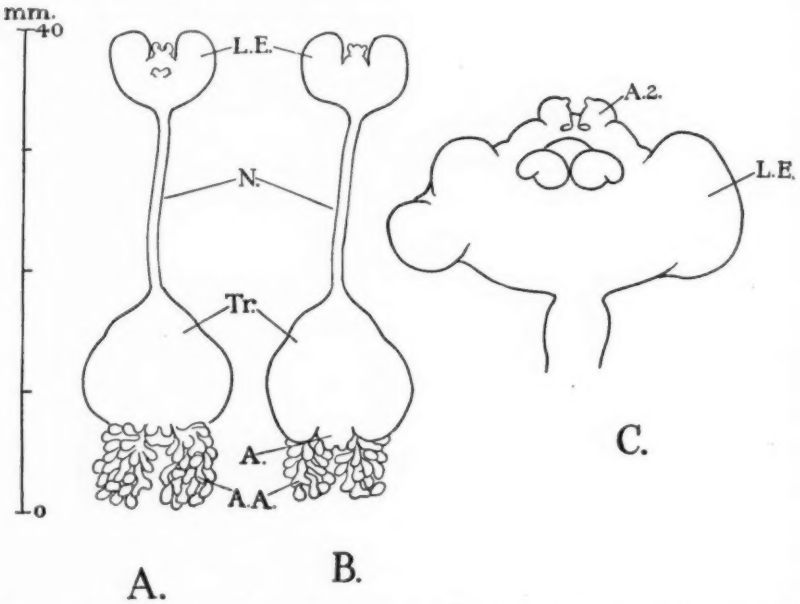

Fig. 1. *Sphyrion lumpi*, ♀. *A*, in ventral aspect; *B*, in dorsal aspect; *C*, enlarged view of head of an older specimen in ventral aspect.

Lettering to Figs. 1–4: *M.* = mouth; *L.E.* = lateral expansions; *N.* = neck; *Tr.* = trunk; *H.* = hump; *A.* = abdomen; *A.A.* = posterior processes; *Os.* = egg-strings; *A* 1. = antennules; *A* 2. = antennae; 2*Mx.* = second maxillae; *Mp.* = maxillipedes.

(*Note.* In Figs. 2 and 3 the head is tilted through 90° towards the spectator so that its ventral edge is superior and its dorsal inferior.)

S. laevigatum Guérin-Méneville (1829).

Material. 1 ♀ (86.53) from *Genypterus blacodes*, New Zealand (Fig. 2).

Dimensions: length of head and neck 22 mm., neck 13 mm. Lateral expansions, width 48 mm. Trunk, length 16 mm., width 24 mm. Posterior processes 25 mm. Egg-strings 98 mm.

Diagnosis. *Cephalothorax* enlarged by enormous lateral expansions with pointed lateral apices till it is twice the width of the trunk, provided with four rounded mammillae placed two on the ventral edge (superior in Fig. 2) and two on the dorsal, the latter being respectively further from the middle

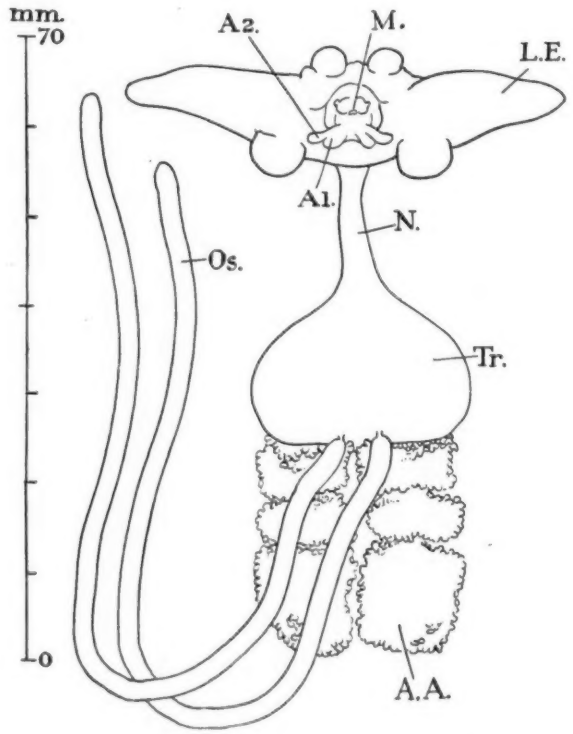

Fig. 2. *Sphyrion laevigatum*, ♀, in dorsal aspect. (Lettering explained under Fig. 1.)

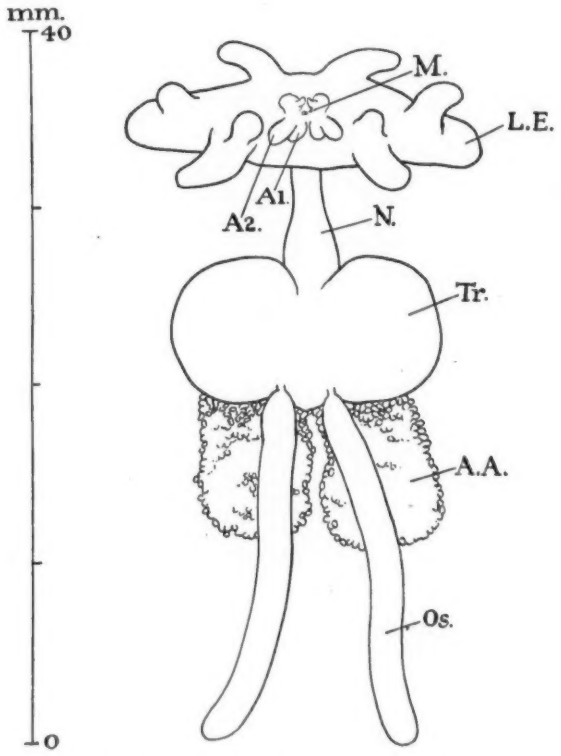

Fig. 3. *Sphyrion kingi*, ♀, in dorsal aspect. (Lettering explained under Fig. 1.)

line of the head than the former. Both pairs of antennae reduced to knobs. *Neck* shorter than trunk. *Trunk* bulbous, much wider than long in the ratio 3 : 2, flattened dorsiventrally, lateral margins rounded, posterior margins straight. Posterior processes very finely branched, only a little less long than trunk and neck together, ramifications in three distinct series. *Abdomen* minute and undivided. *Egg-strings* very long, longer than the whole of the rest of the animal.

Remarks. This is undoubtedly the animal described as *S.* [*Lesteira*] *krøyeri* by Thompson (1890) on *Genypterus blacodes* from New Zealand. It is certainly also that described by Brian (1917) from an unknown host at New Anchor Bay as *S. laevigatum*. There is a probability, but by no means a certainty, that this animal is *S. laevigatum* Guérin-Méneville (1829); but as most modern authors are satisfied with the latter identification I am content to follow them in assigning *S. laevigatum* as having priority over *S. krøyeri* to this species.

S. kingi Cunningham (1871).

Material. 5 ♀♀ (69–37) from Dungeness, two of them headless, presented by the Lords of the Admiralty, collected by Dr Cunningham (Fig. 3).

Dimensions: length of head and neck 12 mm., neck 8 mm. Width of lateral expansions 19·5 mm. Trunk, length 9 mm., width 14·5 mm. Abdomen 2 mm. Posterior processes 8·5 mm. Egg-strings 20 mm.

Diagnosis. *Cephalothorax* enlarged by lateral expansions with broadly rounded lateral apices till it is slightly greater than the width of the trunk, provided with long processes instead of mammillae, four pairs in fixed positions (not mere asymmetrical excrescences), some of which tend to bifurcation in Stebbing's specimen (*vide infra*), two pairs ventral (superior in Fig. 3) (one pair submarginal), two pairs dorsal (one pair submarginal and almost mammillae). The larger processes disposed as the mammillae of *S. laevigatum*. Both pairs of antennae reduced to large knobs. *Neck* a little less than length of trunk, enlarged at its base. *Trunk* bilobed, the swollen base of neck inserted between the lobes in front, much wider than long, lateral and posterior margins both rounded. Posterior processes very finely branched as in *S. laevigatum*, but ramifications *not* in series, less than the length of the trunk. *Abdomen* undivided. *Egg-strings* a little more than twice the length of the posterior processes.

Remarks. Bassett-Smith (1899) queries that these Dungeness specimens are *S. lumpi* but in a MS. note at the British Museum considers them *S. laevigatum*. This species was described by Stebbing (1900) from S. Africa, with an excellent plate, as *S. laevigatum*, and by Quidor (1912) with a photograph of the lateral expansions and their processes as *S. delagei*. In spite of his rather poor figure showing but six marginal processes, where Cuvier and Guérin-Méneville indicate four for *S. laevigatum*, I am satisfied that this is the species described by R. O. Cunningham (1871) as *S. kingi*; accordingly that specific name has priority.

A comparison of the three species of **Sphyrion.**

Species ...	*S. lumpi*	*S. laevigatum*	*S. kingi*
Author ...	(Krøyer 1845)	Guérin-Méneville 1829	Cunningham 1871
Lateral expansions of cephalothorax	(Young) ¾ width of trunk	—	—
	(Old) slightly wider than trunk	Enormous Twice width of trunk	Slightly wider than trunk
Lateral apices	Rounded with a tendency to bifurcation	Pointed	Rounded
Protuberances	None	Two pairs of mammillae	Four pairs of processes
Neck	Much longer than trunk	Shorter than trunk	A little shorter than trunk
	Not swollen at base	Not swollen at base	Swollen at base
Trunk	Obcordate	Bulbous	Bilobed
	Length approx. = width	Length = ⅔ width	Much wider than long
	Post. margins straight	Post. margins straight	Post. margins rounded
Posterior processes	Stout	Very fine	Very fine
	More than ½ length of trunk	In three series	Not in three series
		Much longer than trunk	Less than length of trunk
Abdomen	Bilobed	Minute	—
	Two ventral abdominal appendages	Undivided	Undivided
Egg-strings	—	Much longer than entire length of animal	Stouter—more than twice length of posterior processes

Family LERNAEOPODIDAE Milne-Edwards (1840).

Basanistes hucho (Schrank 1786).

Material. 1 ♀ of this rare and interesting genus and species in an excellent state of preservation from *Salmo huchonis* (Fig. 4).

Dimensions: width (really length) of head 1·5 mm.; length of second maxillae 2·1 mm., of trunk 4 mm., of egg-strings 6·4 mm.

Diagnosis. *Cephalothorax* at right angles to the trunk axis from which it is separated by a distinct neck (Fig. 4, *N.*) of apparently one segment. Dorsal carapace minute. No abdomen, anal laminae or abdominal processes. A large spherical knob or hump on the back of the head (Fig. 4, *H.*), a row of smaller knobs along the mid-dorsal line of the trunk, and a row of three along each lateral margin. *Second maxillae* of a medium length, as compared with *Lernaeopoda* and *Clavella* on either hand, stout, enlarged proximally and inserted at the side of the head, their distal ends expanded into concave discs with thick borders; the bulla is absent in this specimen but from Schrank's figure it possesses an extremely long and narrow pedicel which arises from between the discs whose inner borders are partly in contact with it; in the absence of the bulla the discs are free from one another. *Maxillipedes* stout, standing out well in front of the second maxillae. *Trunk* stout, ellipsoidal, about three times as long as wide. *Egg-strings* elongated, tapering, one and a half times as long as the trunk.

Remarks. Wilson (1915) states there is no neck, and no dorsal carapace; however, I do not think he has examined any species of this genus.

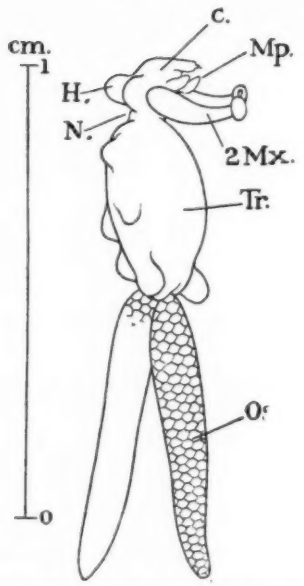

Fig. 4. *Basanistes hucho*, ♀. (Lettering explained under Fig. 1.)

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(*MS. received for publication* 20. II. 1928.—Ed.)

ERRATA. *Parasitology*, vol. XIX. (Paper by W. H. Leigh-Sharpe and C. L. Oakley.)

P. 458, line 26; *for* 460 *read* 464.

P. 460, Fig. 3 B; *for* T_3 *read* T_1.

HELMINTHIC INFESTATIONS OF NATIVES IN THE KENYA HIGHLANDS.

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Introduction.

It is the generally accepted view that the natives of Kenya suffer from some factor, or combination of factors, contributing to poor physical condition and lack of capacity for sustained muscular effort. The Medical Service has been for some years engaged in the investigation of possible causes and contributory factors, approaching the problem from every possible avenue. Among other suggestions that have been made Dr J. L. Gilks, Director of Medical and Sanitary Services, has referred to the possibility of intestinal helminths being concerned in the production of the generally poor physical development of the Kenya native, with particular reference to the high incidence of infection with *Taenia saginata*. It was known then, as a result of our preliminary examination, that hookworm infestations in the Highlands, though of very frequent incidence, were individually extremely light. At a later date observations upon prisoners carried out by Kelly and Henderson gave some evidence that there was an insufficient margin of calcium in the food and that an increase in the blood calcium of prisoners was usually accompanied by an increase in weight. It was thought that *Taenia saginata* might exert some influence on the calcium metabolism of the host and estimations were therefore made of blood calcium of infested prisoners before and after treatment. These results will be published later.

Incidence of Infestations.

The present paper deals chiefly with the incidence of parasitic infestations among the natives of a juvenile reformatory, and the work was made possible through the courtesy of Dr F. J. Carlyle Johnstone, then Medical Officer of Health, Nairobi, who suggested the inmates of the reformatory as suitable subjects for observation.

The institution in question is located some eight miles from Nairobi at an altitude of about 6000 feet, in an area subject to an annual rainfall of approximately 40 inches. The conservancy measures in force consist in the use of well-constructed bucket latrines with concrete floors raised above ground level. The buckets are emptied daily, being disinfected before they are returned, and the faecal material is buried. Soil-contamination, through irregular defaecation among the boys employed on outside work, undoubtedly occurs, but is reduced to a minimum by the normal discipline of the institution.

The normal diet of the boys does not contain any meat, but an occasional issue is made when an ox is destroyed under circumstances permitting its use as food. The meat furnished in this way is thus always that of an adult animal, generally one of considerable age. Such meat rations are cooked in the reformatory kitchens by boiling for a period sufficiently long to ensure that no larval cestodes could possibly survive. The question of meat consumption is of interest in view of the high incidence of *Taenia saginata* infestation among the inmates and the persistence of infestation in boys who have been in confinement for periods extending to several years.

The inmates are natives, aged 8–14 years, drawn from all parts of East Africa and representative of practically every tribe. They are employed in various capacities, a number being engaged in carpentry and similar indoor occupations, while others tend the gardens of the institution and cultivate their own food-stuff crops. There is a small amount of quarrying, building and road maintenance.

Geographical and meteorological conditions in East Africa vary enormously with the altitude and the distance from the coast, but although the inmates of the reformatory are drawn from areas with widely different climates they are at the present time living in a typical Highland environment. It is therefore not remarkable that although almost every intestinal helminth described from man in East Africa is recorded from these boys, individual infestations with parasites such as hookworm are extremely light and not at all comparable with infestations occurring, for example, at the Coast.

Methods of examination employed.

Two methods were employed in the examination of stools, namely, Lane's method, and the examination of a smear from centrifuged material. Specimens were personally collected by one of the writers in small tubes fitted with sampling spoons and numbered labels. The amount of material used in the

examination was that contained in the sampling spoon filled to the top, the excess being removed by drawing the edges of the spoon across the rim of the tube. This quantity was transferred to a centrifuge tube of 25 c.c. capacity and thoroughly comminuted in water by shaking. The tube was next filled with water and spun at a thousand revolutions per minute for one minute. The supernatant fluid was then poured off and a small measured quantity of the deposit removed with a pipette and transferred to a slide. The centrifuge tube was then filled with saturated saline solution and inverted two or three times to agitate the sediment. It was finally filled to the brim with a pipette, and a large cover-glass was placed over the mouth of the tube in contact with the fluid. The material was then spun at a thousand revolutions for two minutes. The cover-slip was removed together with the adherent drop of fluid and transferred to a slide, upon which it was supported in the usual way by cones of plasticine, the drop being allowed to form a meniscus between the slide and the cover-slip.

Lane's method was selected on account of its usefulness in the detection of the very lightest nematode infestations. A strictly accurate measurement of the quantity of faeces employed was not thought necessary, since it was proposed to subject a number of the patients with hookworm to anthelminthic treatment, repeated if necessary until they became negative, and to recover all the worms passed after treatment. It was considered that more reliable data would be obtained in this way than by the use of any egg-counting method followed by a computation of the number of parasites present. Stoll (1923), and others examine a definite quantity of faecal material, making use of dilution methods, and estimate the number of worms present from the number of eggs passed. One of us has had considerable experience in the examination of faeces from domesticated animals and has failed to obtain consistent results by any of these methods. It was concluded, therefore, that there was considerable variation in the number of eggs excreted from day to day and the experience of Veglia (1927) supports this conclusion. Veglia infected lambs by administering the larvae of *Oesophagostomum columbianum*, and cultivated the larvae from 1 gm. of each day's faeces during the existence of the infestation. The total quantity of faeces passed daily was ascertained by weighing, and the total number of eggs voided was calculated. During the period of maximum oviposition the number of eggs passed daily varied from a maximum of 4,500,000 to a minimum of 500,000. These striking variations in the daily output do not appear to correspond with any change in the consistency of the faecal material. It was decided, therefore, to rely on Lane's method for the detection of the lightest nematode infections and to examine a smear from the first centrifugalisation to detect cestode and trematode eggs and the larvae of *Strongyloides*. A certain number of cestode infestations, especially if they are heavy, can be detected in the flotation preparation but the majority are only revealed in the examination of the smear from the deposit. There are still other infestations with *Taenia saginata*

which are not detected at all by microscopic examination, but are only discovered when a whole stool is searched for the presence of segments. For example, out of 64 hookworm patients who were negative to *Taenia* by microscopic examination, 24 proved to be infested with *Taenia saginata* when whole stools were examined after anthelminthic treatment. In this connection the results of Callanan (1926) are of interest: As the result of a series of faecal examinations upon a batch of hospital patients Callanan formed the opinion that three examinations on separate occasions are necessary for the detection of parasitic infestations.

The results of a preliminary faecal examination of the reformatory inmates are shown in Table I.

Table I.

Result of Preliminary Faecal Examination. (*Microscopic only.*)

Number of Boys examined, 152.

Ascaris lumbricoides	5 = 3·3 %	*Taenia saginata*	24 = 15·8 %
Oxyuris (*Enterobius vermicularis*)	2 = 1·3 %	*Hymenolepis nana*	2 = 1·3 %
Whipworms. *Trichuris trichiura*	55 = 36·27 %	*Schistosoma mansoni*	3 = 2 %
Hookworms	89 = 57·9 %	Negative	38 = 25 %
Strongyloides stercoralis	3 = 2 %		

Single Infections. Total 58.

Ascaris lumbricoides	Nil	*Taenia saginata*	9
Oxyuris (*Enterobius vermicularis*)	1	*Hymenolepis nana*	Nil
Whipworms. *Trichuris trichiura*	10	*Schistosoma mansoni*	Nil
Hookworms	38	Negative	—
Strongyloides stercoralis	Nil		

Double Infections. Total 44.

Hookworm and *Taenia saginata*	6	Hookworm and *Oxyuris*	1
Hookworm and *Trichuris*	30	*Ascaris* and *Trichuris*	1
Hookworm and *Ascaris*	3	*Taenia* and *Trichuris*	1
Hookworm and *Schistosoma mansoni* ...	1	*Trichuris* and *Hymenolepis nana*	1

Triple Infections. Total 11.

Hookworm, *Trichuris*, and *Taenia saginata*... ...	5
Hookworm, *Trichuris*, and *Schistosoma mansoni* ...	1
Hookworm, *Trichuris*, and *Strongyloides*	2
Taenia, *Schistosoma mansoni* and *Trichuris*... ...	1
Hookworm, *Trichuris*, and *Ascaris*	1
Trichuris, *Taenia*, and *Strongyloides*	1

Quadruple Infection.

Hookworm, *Trichuris*, *Taenia saginata* and *Hymenolepis nana*. ... 1

Anthelminthic Treatment.

It was decided to submit a number of boys infested with hookworm alone to anthelminthic treatment with a view to ascertaining the heaviness of individual infestations, the efficacy of carbon tetrachloride against hookworms, and the possible effects upon the physical condition of the patients of the removal of the parasites.

Carbon tetrachloride was introduced as an anthelminthic by Hall (1921), who advocated its trial in the treatment of human hookworm disease as the result of carefully controlled experiments on dogs. In Hall's observations, carbon tetrachloride showed 100 per cent. efficacy against hookworms when given in capsule in doses of 0·3 c.c. per kilogram of body weight as against a maximum efficacy of 54 per cent. for chloroform, 74 per cent. for oil of chenopodium, and 89 per cent. for a mixture of chloroform and chenopodium. Subsequent to these observations carbon tetrachloride has been largely used in the treatment of hookworm disease in the silver fox, and the results have been controlled by post-mortem examination of the animals after destruction for pelting. In doses of about 25 c.c. the drug shows an efficacy of 100 per cent. against the blood-sucking strongyles of the horse, but fails to show any activity against the cyclicostomes and oxyurids of that animal, which however are removed by chenopodium. Hall found that in doses of 0·3, 0·2, and 0·13 c.c. per kilo of body weight, the drug removed all the hookworms present in lightly infested sheep. As the result of experiments carried out by one of us, carbon tetrachloride has been extensively used in the treatment of hookworm disease of sheep in Kenya, a dose of 0·1 c.c. per pound of body weight showing an efficacy of from 97 to 100 per cent. against the sheep hookworm, *Bunostomum trigonocephalum*. More recently, the drug has been used on the recommendation of Montgomerie (1926) in the treatment of liver-fluke, *Fasciola hepatica*, in sheep.

Macht and Finesilver in 1922 demonstrated the value of magnesium sulphate in diminishing or preventing the absorption of other drugs from the alimentary canal. Acting on this information, Hall in 1925 showed that the simultaneous administration of magnesium sulphate will reduce the toxic action of carbon tetrachloride upon dogs without impairing its anthelminthic efficacy. Daubney (1927) has shown that the drug, when given by stomach tube to sheep at the rate of 0·1 c.c. per pound body weight, may produce a mortality of about 33 per cent. when the animals are heavily infested with hookworms, possibly as a result of the innumerable small haemorrhages of the mucous membrane associated with such heavy infestations. The simultaneous administration of two to three ounces of magnesium sulphate in saturated solution entirely prevents mortality and the anthelminthic efficacy of the carbon tetrachloride is not decreased.

On the basis of Hall's observations the dose suggested for man was about 3 c.c. and a considerable number of treatments have been carried out. Lambert in 1922 and 1923, treated 42,000 patients without the development of any serious symptoms. The dose given was 0·2 c.c. per year of age up to 15 years and from 3 to 4 c.c. for adults. Of a further batch of 8000 cases similarly treated three patients died, but the carbon tetrachloride was found to be impure. The post-mortem changes were acute hepatitis and necrosis of the liver, and Lambert remarked that the first of the three patients to die had a heavy infestation with *Ascaris*. Five other patients, who became seriously ill,

all had infestations of over 100 ascarids. In controlled experiments Lambert found the drug to have an efficacy of 96 to 100 per cent. against hookworm, 40 per cent. against *Ascaris* and only slight efficacy against whipworm. As contra-indications to the administration of carbon tetrachloride, he mentions constipation, and the taking of food either just before or after treatment. Headaches not infrequently follow the administration of the drug, but are rare when magnesium sulphate is given simultaneously. Lambert did not find that simultaneous administration of the saline purge decreased the efficacy of the carbon tetrachloride, but considers, however, that the dose of 3 to 4 c.c. for adults is larger than desirable. O'Brien (1925) has reported upon 225,000 cases treated with a mixture of 40 per cent. oil of chenopodium and 60 per cent. carbon tetrachloride given in a dose of 2 c.c. Three deaths occurred as a result of the treatment. Day (1924) and Khalil (1926) have used carbon tetrachloride in Egypt, the former in a dose of 3 to 5 c.c. and the latter in one of 5 c.c. One sample used by Khalil was found to be toxic and although impurities could not be detected, tests showed that the toxic properties were confined to the first part of a fractional distillate. Subsequent examination by Dale and King showed that sulphur compounds distil over with this fraction. In sulphur-free samples of carbon tetrachloride this first portion of the distillate proved to be non-toxic when tested upon experimental animals. Höppli and Kesler (1924) state that impure samples of carbon tetrachloride give rise to liver lesions when administered to dogs in therapeutic doses.

At the present time the drug is being largely used in the treatment of hookworm disease, but is held by many to be unsafe in the usual therapeutic doses. We have treated some 250 natives of all ages in a series of controlled investigations, with a minimum dose of 1·5 c.c. for children of ten years and a regular adult dose of 4 c.c., without any fatalities. In one instance, which was attributed to idiosyncrasy, a condition approximating to profound anaesthesia was produced; but recovery was rapid after the administration of artificial respiration, and no subsequent systemic effects were noted. The patient collapsed soon after the administration of the drug but was practically well next day. This case was reported by one of us (Carman, 1926).

Methods of treatment and examination employed.

Patients to be treated with carbon tetrachloride were fasted from mid-day on the previous day to 7 a.m. on the day of treatment and were then given their dose without any vehicle or containing capsule. The treatment was followed at varying intervals by one ounce of magnesium sulphate in saturated solution. When treating adults, the amount of Epsom salts was increased to three ounces, also given in saturated solution. The patients remained under the personal observation of one of us until each had passed a stool into his numbered receptacle. The boys were then confined in a building by themselves and all stools passed were collected daily for a further period of three days.

Later, when it was found that no worms were passed on the fourth day, the stools were collected and examined for three days only.

Stools for examination were comminuted in a 5 per cent. watery solution of carbolic acid and allowed to stand for a few minutes to render them less offensive, after which they were washed with a hose through two screens of twenty and sixty meshes to the inch respectively. The material retained by the screens was finally transferred in water to tall sedimenting jars, and the sediment was examined in small quantities in a flat-bottomed glass dish. It was found to be of advantage to examine the material against a black and white ground and to hold the dish about an inch above the background. The task of examining the stools was rendered much more tedious by their bulk and by the presence of large quantities of undigested grain and fibre, even in the first stool passed after fasting. The grain—maize and beans—was frequently passed intact without the slightest evidence of any attempt at mastication, and it was not uncommon for a stool to contain whole grain sufficient to fill a ten ounce measure glass. In addition to this whole grain a large quantity of husk and broken grain was present. The fibre so constantly seen was that of the sugar-cane, which is habitually eaten in the raw state. When passed in the stool it is usually in a tangled ball in which the entire strobila of a tapeworm may be enmeshed, adding materially to the difficulty of the search for scolices or for small worms such as oxyurids or hookworms. One week after the administration of carbon tetrachloride a preparation of faeces by Lane's method was examined for hookworm eggs; and in cases where tapeworm had been seen, a whole stool, obtained by purgation, was examined after a further interval of at least seven weeks.

Results.

Detailed results of treatment are appended in the form of Case Records, pp. 198–205, from which the chief points are selected for discussion below.

Taking the whole series of 67 boys for whom complete records are available, the efficacy of carbon tetrachloride against hookworm, based on the result of examination of the faeces by Lane's method, is 76·1 per cent. of complete cures. While the batch of ten boys treated with the smaller doses of carbon tetrachloride showed only six complete cures, the difference between this result and that of the whole series, cannot be considered significant. Similarly, the batch of ten treated with 4 c.c. of carbon tetrachloride does not show an appreciably greater proportion of cures. In the same way, it is seen from the records that it does not appear to make any difference to the success of the treatment whether the purgative is given immediately, or after an interval of up to two hours. Most of the parasites are passed on the second day, and none, with the exception of partly digested fragments of tapeworm, on the fourth day after treatment. No record is therefore given of the fourth day's examination.

The first point of importance brought out by the treatment is the lightness

of the individual infestations with hookworm. In only two cases were more than twenty parasites collected after treatment. The average infestation seems to be less than ten, and this finding is in accord with post-mortem findings in the Highlands. This may account also for the comparatively low percentage of complete cures (76·1) effected by the treatment, the general experience being that very light infestations with hookworm are more difficult to cure than are heavy ones. When the high incidence of hookworm among the inmates of the reformatory is taken into consideration, it seems reasonable to conclude that hookworm disease is not at present a serious menace to the health of the native community in the Highlands. This conclusion is further borne out by the records of weight increase among patients given below.

Another striking feature of the results, to which reference has already been made, is the high incidence of infestations with *Taenia*, many of which escape notice during careful microscopic examination of stools. Of 64 patients treated for hookworm, whose faeces had been negative for *Taenia* at the microscopic examination, 24 proved to be infested with *Taenia saginata* when whole stools were examined. The original microscopic examination resulted in the detection of 24 infestations with *Taenia* out of 152 boys examined, but examination of a whole stool shows that 24 out of 64 negatives, that is approximately 37·5 per cent., were also infested. The actual incidence of tapeworm among the reformatory inmates is therefore approximately 50 per cent. Thus the microscopic examination of faeces by direct centrifuge and by Lane's method failed to reveal about 30 per cent. of the total infestations with *Taenia*. These results are not surprising when one remembers that the parasite is without an orifice for oviposition. In view of the rapidity with which *Taenia saginata* grows, liberating, when mature, numbers of gravid segments every day, it might be expected that examination by washing a whole stool after purgation would prove a fairly reliable method of diagnosis. Our records indicate that this is the case, since of a total of 172 cases of *Taenia* infestation tabulated in this paper only 11, or 6·4 per cent., failed to show segments in the first stool passed after treatment for hookworm. Very few patients passed strobilae in this stool, the anthelminthic effect of the carbon tetrachloride being manifested mainly on the second day. The incidence of infestation among the boys examined is not astonishing when one realises that more than 50 per cent. of calves brought to post-mortem examination in the Nairobi slaughter-houses are condemned on account of measles, a much higher incidence than has ever been observed in European abattoirs. The meat killed for Europeans in Nairobi itself is drawn chiefly from stock farms under European control and it will be evident that the percentage of infested animals is likely to be much higher among native-owned cattle in the reserves. Since such native cattle are eaten without any regard for the presence or absence of measles it is not surprising that in some areas practically every individual is reputed to be infested with *Taenia*. It might be remarked that the incidence of infestation among inmates who had been confined in the

reformatory for periods of less than one year is approximately 70 per cent., but in boys with a residence of three years and upwards the infestations amount to less than 20 per cent. of the total.

The third point of interest brought out by our investigation was the frequency with which boys treated primarily for hookworm passed strobilae of tapeworm, and it was decided to examine whole stools of all patients found to be infested with *Taenia* after a minimum interval between treatment and final examination of at least seven weeks, in order to estimate the percentage of actual cures. After the period stated all the boys were given a heavy saline purge and whole stools were searched for *Taenia* segments. Of 30 cases so treated, only one was found to be positive, though only two scolices were identified during the original investigation after treatment with carbon tetrachloride. This gives the remarkable efficacy for this drug against *Taenia saginata* of nearly 97 per cent. Manson-Bahr (1925, p. 571) refers briefly to the fact that carbon tetrachloride anaesthetises tapeworms, but the writers have been unable to find any other reference in the literature to this anthelminthic property of the drug. That carbon tetrachloride is effective against some trematodes has been noted above in a reference to its action on *Fasciola hepatica*, the liver-fluke of sheep. As observed by Hall (1923) and Daubney (1926) the drug will also remove certain cestodes of sheep, notably *Avitellina centripunctata*, while it is useless against other cestodes of sheep or against the cestodes of dogs.

In every instance in which a strobila was passed by our patients after the administration of carbon tetrachloride, the parasite was dead as shown by its colour, lack of contractility, and the rapidity with which digestion set in. In a large number of cases the worms were in a fairly advanced state of digestion; this may explain our inability to identify the heads.

In the light of these findings it was thought desirable to treat a number of patients specifically for Taeniasis, and for this purpose the prisoners in Nairobi gaol were used. Eighty-two cases were treated in batches of twelve, practically the same routine being adopted as that described above for the reformatory. The dose of carbon tetrachloride given was one fluid drachm (4 c.c.) with 20 minims of oil of chenopodium, combined as a draught, and followed at once by three ounces of magnesium sulphate in saturated solution. It will at once be apparent from the tabulated case records that the individual infestations of these prisoners were much heavier than those of the reformatory inmates, and that the removal of two or even more heads does not imply that a cure has been effected in any case. Moreover, the fact that no scolex has been found in the stools does not necessarily mean that heads have been retained. Throughout the whole series of examinations a large quantity of almost completely digested fragments of tapeworm was constantly present in the later stools. The scolices collected were in all stages of disintegration and only those that could be identified with certainty are included in our records. It must be concluded that many of the heads were so digested as to escape

detection. The heaviness of the individual infestations, as evidenced by the fact that three or more heads were recovered from each patient in four cases and by the finding of several strobilae with definite necks in one stool, appears to be responsible for the decreased efficacy of carbon tetrachloride among this batch of patients. Of the first 70 convicts 62 remained in gaol long enough for the final stool examination to be carried out, and of these 36 proved to be negative. The efficacy of the drug in this batch was therefore 58 per cent. In a further batch of twelve cases, the patients were subjected to preliminary purgation with castor oil and were given fluid diet before treatment. It was thought possible that if the gut could be cleared prior to treatment of the usual mass of undigested grain and husk, the efficacy of the anthelminthic might be increased and the task of stool examination would certainly be lightened. The patients were therefore admitted to hospital a day earlier than usual and, after a heavy dose of castor oil, were kept on liquid diet until starved before treatment. They were then treated in exactly the same way as the other 70 patients, but in spite of the fact that seven scolices were collected from five of them, none of the eleven who remained in gaol until the next stool examination after seven weeks proved to be cured. This result suggests that while the preliminary administration of castor oil rendered the detection of heads more easy, the anthelminthic efficacy of the carbon tetrachloride was materially diminished. Though this suggestion requires further confirmation, it appears that purgation with castor oil should be avoided before treatment of Taeniasis with carbon tetrachloride.

The Influence of Infestations and of Treatment upon Physical Condition.

One of the objects of this investigation was to obtain, if possible, some data as to the responsibility of different parasitic infestations for any loss of physical condition, or retarded development among natives in the Kenya Highlands. It was thought that any such effect would be more evident among the growing inmates of the reformatory than among adults. The weight and height of each boy has been recorded monthly, commencing eight months before any treatment was carried out; and it is therefore possible to compare rates of growth and increase in weight over a considerable period in boys free from the major parasitic infestations and in those infected, and in the case also of the latter before and after anthelminthic treatment. (Table II.)

So far as boys infested with hookworm alone, or with hookworm and parasites other than *Taenia saginata*, are concerned, there is no appreciable improvement after treatment, nor any difference between their average monthly weight increase and that of negative patients; which is not surprising when the lightness of the individual infestations is taken into consideration. The evidence supports the prevalent view, which has however been strongly contested by Lane, Lambert and others, that small infestations of ten or less hookworms are comparatively harmless to the individual.

Table II.

Average increase in weight in pounds per month of a number of Boys grouped according to Helminthic Infestations.

		Taenia and Hookworm		Hookworm without *Taenia*		
Negative	*Taenia* only Untreated	(1) Before treatment	(2) After treatment	(1) Before treatment	(2) After treatment	(3) Untreated
lb.	lb.	lb.	lb.	lb.	lb.	lb.
1·050	1·125	0·570	0·910	0·125	0·410	0·570
0·730	0·047	0·285	0·500	0·333	1·160	0·630
0·950	0·860	1·400	0·000	0·900	0·250	3·222
0·900	1·000	0·111	0·583	0·900	1·080	0·750
0·666	1·000	0·444	0·916	1·222	1·000	0·728
1·380	0·620	1·111	0·410	0·500	0·333	1·333
0·666	0·710	0·500	1·000	0·166	0·930	0·400
0·190	0·476	0·000	1·080	0·500	0·160	1·240
0·4375	0·570	0·500	2·080	0·750	0·280	0·777
0·900	1·333	1·000	0·666	1·250	1·160	0·666
0·810	1·090	0·875	1·125	1·250	1·000	0·777
0·666	0·860	0·000	1·150	0·750	0·610	1·000
0·900	0·710	0·375	0·555	0·857	1·080	0·430
0·470	1·090	1·125	1·700	1·433	1·500	1·000
1·310	0·333	0·750	0·540	1·000	1·700	1·333
1·270	0·315	1·250	1·580	0·000	1·375	0·500
0·666	0·390	0·625	0·460	0·430	0·111	
0·780		0·125	1·750	0·710	0·375	
1·166		0·710	0·930	0·833	1·000	
0·333		1·144	1·444	1·000	0·930	
0·610		0·333	0·750	0·833	1·230	
0·700		0·144	0·000	1·125	1·600	
0·888		0·166	1·125	0·750	1·250	
0·280		0·870	1·270	0·333	0·333	
0·380		0·833	1·400	1·000	1·000	
0·620		0·000	1·466	0·333	0·888	
0·222		0·500	1·000	0·500	0·710	
1·083		0·666	2·500	1·500	1·750	
0·625				1·500	0·500	
1·625				1·000	1·090	
0·710						
0·666						
0·400						
0·170						
0·500						
0·500						
1·100						
No. of Boys 37 | 27·3195	17 | 10·529	28 | 16·412	28 | 28·890	30 | 22·783	30 | 26·235	16 | 15·356
Mean increase 0·7384	0·619	0·586	1·031	0·7594	0·8745	0·959
(lb. per month)						

	lb.
Negative, 37 cases—average gain per month	0·7384
Taenia (untreated), 17 cases—average gain per month	0·619
Taenia and Hookworm (before treatment), 28 cases—average gain per month	0·586
Taenia and Hookworm (after treatment), 28 cases—average gain per month	1·031
Hookworm without *Taenia* (untreated), 16 cases	0·959
Hookworm without *Taenia* (before treatment), 30 cases	0·7594
Hookworm without *Taenia* (after treatment), 30 cases	0·8745

When, however, the records of patients carrying *Taenia saginata* are examined, one finds some evidence that the parasite is responsible for retardation of growth. If the rate of increase in weight of the negative cases is taken as normal, then, prior to treatment, patients infested with *Taenia saginata* appear to have been progressing at a sub-normal rate. When a further comparison is made between the monthly increase in weight of the latter group before and after anthelminthic treatment it is at once evident that the removal of *Taenia saginata* has been followed by a very definite acceleration of the normal weight curve. The average monthly increase of body weight of 47 patients infested with *Taenia* was 0·616 lb., while that of 28 of these boys subsequently treated was 0·586 lb. before treatment. After treatment, resulting in approximately 97 per cent. of cures for tapeworm, the average monthly increase in weight of these 28 patients was 1·031 lb. Nineteen boys infested with *Taenia*, two of whom were also carrying hookworm, remained untreated, and together with the 37 negatives and 46 cases infested with hookworm, served as controls against the possibility of the increase being due to some common factor other than the removal of *Taenia*. The figures have been submitted to Mr A. Walter, the Statistician to the Governors' Conference, who has very kindly examined them by the usual statistical methods. The standard deviation of the difference of the mean increases in weight before and after treatment of the 28 patients treated for *Taenia* have been taken by the formula $\sqrt{\frac{\sigma a^2}{N} + \frac{\sigma b^2}{N}}$, where the standard deviations σa and σb have been determined from the samples themselves.

Monthly weight increase of 28 *patients infected with* Taenia.

(*a*) Before treatment, average weekly increase		0·586 lb.
(*b*) After treatment, average weekly increase		1·031 lb.
(*c*) Difference between means		0·445 lb.
Number of cases, 28 = *N*.		
Standard deviation of (*a*)	$\sigma a = 0{\cdot}400$.	
Standard deviation of (*b*)	$\sigma b = 0{\cdot}572$.	
Standard deviation of (*c*)	$\sigma c = 0{\cdot}131$.	

Comparing the difference (*c*) of 0·445 lb., with its standard deviation of 0·131, the ratio is in excess of 3 : 1, which is generally accepted as a significant figure.

General Discussion.

The number of samples available for statistical treatment is small and it seems probable that a considerable increase in the numbers treated would result in the production of even more definite evidence that *Taenia saginata* is capable of retarding the growth of young natives.

Further, the extremely high incidence of this infestation among East African natives would appear to justify expenditure of public funds on its control. Control of infestation with *Cysticercus bovis* in cattle, in the absence

of efficient meat inspection, which is obviously impossible for some years in the native reserves, must rest largely upon educational methods which point out the undesirability of indiscriminate defaecation in the neighbourhood of cattle bomas and upon heavily grazed pasture land. This, and instruction as to the necessity to cook thoroughly all beef, can conveniently be combined with mass anthelminthic treatment.

In the second series of boys, treated at the Prison, the carbon tetrachloride was combined with oil of chenopodium largely because of the well-established efficacy of the latter drug against *Ascaris* and *Oxyuris*. The results indicate that in the combination, which contained somewhat larger doses than are usually administered, neither of the drugs was decreased in efficacy. Since carbon tetrachloride gave an efficacy of 97 per cent. in boys lightly infested with *Taenia saginata* and 58 per cent. in extremely heavy infestations, while continuing to manifest its usual activity against hookworms, it appears to the writers to constitute the most reliable of the economically practicable treatments for *T. saginata*. The combination of carbon tetrachloride and oil of chenopodium constitutes a fairly cheap and easily administered anthelminthic possessing a high efficacy against *T. saginata*, hookworms, ascarids and oxyurids, that is to say against the four most important helminths of man of East Africa.

SUMMARY.

(1) Examination of the inmates of Government reformatories in the Highlands of Kenya showed a high incidence (57·9 per cent.) of very light infestations with hookworm, and an incidence of approximately 50 per cent. of *Taenia* infestations. Many of the latter are not detected by the usual microscopic examination.

(2) Treatment with carbon tetrachloride in doses of from 1½ c.c. for children to 4 c.c. as the standard adult dose gave approximately 76·1 per cent. cures for hookworm, and in the case of boys with fairly light infestations with *T. saginata* an efficacy of approximately 97 per cent. In the case of 72 boys very heavily infested with *Taenia* 58 per cent. cures were effected by a single treatment with carbon tetrachloride and oil of chenopodium.

(3) A combination of carbon tetrachloride and oil of chenopodium appears to be a safe and efficacious anthelminthic for the common worm infestations of man in Kenya.

(4) Growing natives lightly infested with hookworm appeared to grow and increase in weight at a normal rate, and did not improve in physical condition after treatment.

(5) Boys in the same institution infested with *Taenia* progressed at a subnormal rate, but increased to a figure above normal after treatment, the increase appearing to be mathematically significant in spite of the small number of samples analysed.

CASE RECORDS.

KABETE REFORMATORY.

Batch 1.

Treated 9. vii. 26. Dose of CCl_4 graded according to size and physical condition. Mag. sulph. given at once.

No.	Ref'y no.	Preliminary faecal examination	Treatment	Worms passed			Examination a week after treatment by Lane's method only
				1st day	2nd day	3rd day	
1	410	Hookworm	2 c.c. CCl_4	Negative	71 *Necator*	Negative	Negative
2	505	Hookworm	2 c.c. CCl_4	*Taenia* segments	*Taenia* segments	Negative	Negative
3	506	Hookworm, light, *Trichuris*, *Heterodera*	1½ c.c. CCl_4	Negative	2 *Necator*, 1 *Ancylost*	Negative	Hookworm eggs
4	518	Hookworm, heavy	2 c.c. CCl_4	*Taenia* strobila	*Taenia* strobila	Negative	Hookworm eggs
5	563	Hookworm	2 c.c. CCl_4	Negative	1 *Necator*	Negative	Negative
6	565	Hookworm	2 c.c. CCl_4	*Taenia* segments	2 *Necator*, *Taenia* strobila	Negative	Negative
7	566	Hookworm	2 c.c. CCl_4	Negative	Negative	Negative	Negative
8	568	Hookworm	2½ c.c. CCl_4	Negative	Negative	Negative	Negative
9	578	Hookworm	2 c.c. CCl_4	Negative	Negative	Negative	Negative
10	653	Hookworm	2 c.c. CCl_4	Negative	7 *Necator*	Negative	Negative

Batch 2.

Treated 16. vii. 26. All received 3 cc. CCl_4 followed by mag. sulph. oz. 1 in saturated solution.

No.	Ref'y no.	Preliminary faecal examination	Worms passed			Examination a week after treatment by Lane's method only
			1st day	2nd day	3rd day	
1	472	Hookworm, light	*Taenia* segments	4 hookworms, *Taenia* segments	Negative	Negative
2	473	Hookworm, light, *Heterodera*	Negative	2 hookworms	Negative	Negative
3	516	Hookworm, light	Negative	4 hookworms, *Taenia* segments	Negative	Negative
4	539	Hookworm, very light	*Taenia* segments	1 hookworm, *Taenia* strobila	1 hookworm, *Taenia* segments	No hookworm eggs
5	564	Hookworm, *Trichuris*	Negative	Negative	3 hookworms	No hookworm eggs
6	574	Hookworm, *Trichuris*	Negative	Negative	Negative	No hookworm eggs
7	569	Hookworm, very light	Negative	Negative	Negative	Hookworm, *Trichuris*
8	576	Hookworm, apparently heavy, *Trichuris*	Negative	11 hookworms	Negative	No hookworm eggs
9	579	Hookworm, light, *Trichuris*, *Taenia*	*Taenia* segments	2 hookworms, 1 *Oxyuris*, *Taenia* strobila	Negative	Hookworm, *Trichuris*

Batch 3.

Treated 31. viii. 26. All received 3 c.c. CCl_4 followed by mag. sulph. oz. 1 in saturated solution after an interval of 10 minutes.

No.	Ref'y no.	Preliminary faecal examination	Worms passed			Examination a week after treatment by Lane's method only
			1st day	2nd day	3rd day	
1	504	Hookworm, *Trichuris*	Negative	Negative	Not examined	Discharged from reformatory
2	513	Hookworm, *Taenia*	*Taenia* segments	Negative	Not examined	Negative
3	547	Hookworm, *Trichuris*	4 *Necator*, 2 *Oxyuris*	1 *Necator*	Not examined	Discharged from reformatory
4	550	Hookworm	Negative	Negative	Not examined	No hookworm eggs
5	552	Hookworm, *Trichuris*, *Schistosoma mansoni*	Negative	2 *Necator*	Not examined	Hookworm, *Trichuris*, *Schistosoma mansoni*
6	554	Hookworm, *Trichuris*, *Heterodera*	Negative	3 *Necator*	Not examined	Hookworm, *Trichuris*
7	558	Hookworm, fairly heavy, *Trichuris*	*Taenia* segments	Negative	Not examined	No hookworm eggs
8	561	Hookworm, *Ascaris*, *Oxyuris*	Negative	1 *Necator*	Not examined	No hookworm eggs
9	571	Hookworm, *Trichuris*	Negative	9 *Necator*	Not examined	No hookworm eggs
10	573	Hookworm, *Oxyuris*	Negative	7 *Necator*	Not examined	No hookworm eggs

KABETE REFORMATORY—*continued.*

Batch 4.

Treated 7. ix. 26. All received 3 c.c. CCl_4 followed by mag. sulph. oz. 1 in saturated solution after an interval of 30 minutes.

No.	Ref'y no.	Preliminary faecal examination	Worms passed			Examination a week after treatment by Lane's method only
			1st day	2nd day	3rd day	
1	582	Hookworm, light	Negative	*Taenia* segments	Negative	Negative
2	585	Hookworm, very light	Negative	Negative	2 hookworms	Negative
3	598	Hookworm, *Trichuris*	Negative	1 *Oxyuris*	Negative	Hookworm, *Trichuris*
4	599	Hookworm, light	Negative	Negative	9 hookworms	Negative
5	600	Hookworm, apparently fairly heavy, *Heterodera*	Negative	19 hookworms	Negative	Negative
6	601	Hookworm, very light, *Trichuris*, *Heterodera*	Negative	1 hookworm	1 hookworm	Negative
7	606	Hookworm, apparently fairly heavy, *Trichuris*, *Heterodera*	*Taenia* segments	*Taenia* strobila, 1 *Oxyuris*, 11 hookworms	Negative	Hookworm, very light
8	608	Hookworm, light, *Trichuris* *Heterodera*	Negative	2 hookworms	2 hookworms	No hookworm eggs
9	609	Hookworm, light	Negative	9 hookworms	Negative	Negative
10	613	Hookworm, apparently heavy, *Trichuris*	*Taenia* segments	*Taenia* strobila, 18 hookworms	2 hookworms	No hookworm eggs

Batch 5.

Treated 14. ix. 26. All received 3 c.c. CCl_4 followed by mag. sulp. oz. 1 in saturated solution after an interval of 30 minutes.

No.	Ref'y no.	Preliminary faecal examination	Worms passed			Examination a week after treatment by Lane's method only
			1st day	2nd day	3rd day	
1	614	Hookworm	Negative	*Taenia* head, 4 hookworms	*Taenia* head, 2 *Oxyuris*	Negative
2	616	Hookworm, light, *Taenia*	*Taenia* segments	Negative	Negative	Negative
3	620	Hookworm, light, *Trichuris*, *Heterodera*	*Taenia* segments	*Taenia* neck, 1 hookworm	*Taenia* segments, 1 hookworm	No hookworm eggs
4	622	Hookworm, light	Negative	1 hookworm	Negative	No hookworm eggs
5	623	Hookworm, light, *Trichuris*	Negative	3 hookworms	Negative	Hookworm, *Trichuris*
6	624	Hookworm, *Heterodera*,	*Taenia* segments	*Taenia* segments, 3 hookworms	Negative	Hookworm
7	625	Hookworm, light	*Taenia* segments	*Taenia* segments, 1 *Oxyuris*, 5 hookworms	*Taenia* segments, 1 hookworm	Negative
8	626	Hookworm, *Trichuris*, *Ascaris*, heavy	Negative	Negative	Negative	No hookworm eggs
9	627	Hookworm, light, *Trichuris*	*Taenia* segments	*Taenia* segments	Negative	No hookworm eggs
10	630	Hookworm, *Taenia*	*Taenia*	Negative	Negative	No hookworm eggs

Batch 6.

Treated 21. ix. 26. All received 3 c.c. CCl_4 followed by mag. sulph. oz. 1 in saturated solution after an interval of 2 hours.

No.	Ref'y no.	Preliminary faecal examination	Worms passed			Examination a week after treatment by Lane's method only
			1st day	2nd day	3rd day	
1	632	*Trichuris*, Hookworm	*Taenia* segments	*Taenia* strobila, 34 hookworms	Negative	No hookworm eggs
2	640	Hookworm, light	Negative	Negative	Negative	Negative
3	641	Hookworm, *Trichuris*	*Taenia* segments	6 hookworms	Negative	No hookworm eggs
4	644	Hookworm, light, *Heterodera*	Negative	*Taenia* segments	Negative	No hookworm eggs
5	648	Hookworm, *Heterodera*	Negative	*Taenia* segments, 2 hookworms	2 hookworms	No hookworm eggs
6	649	Hookworm, *Trichuris*	Negative	2 hookworms	Negative	Negative
7	650	*Trichuris*, *Taenia*, *Heterodera*, Hookworm, light	*Taenia* segments	Negative	Negative	No hookworm eggs
8	651	Hookworm, light, *Trichuris*	Negative	Negative	Negative	No hookworm eggs
9	656	Hookworm, light, *Taenia*, *Heterodera*	*Taenia* segments	*Taenia* strobila, 1 hookworm	Negative	Hookworm, *Trichuris*, *Heterodera*
10	658	Hookworm, *Trichuris*	Negative	Negative	Negative	No hookworm eggs

KABETE REFORMATORY—*continued.*

Batch 7.

Treated 28. ix. 26. All received 4 c.c. CCl_4 followed by mag. sulph. oz. 1 in saturated solution at once.
(N.B. No. 3, about an hour after treatment began to feel ill, became rapidly unconscious, stopped breathing, and was only revived with difficulty.)

No.	Ref'y no.	Preliminary faecal examination	Worms passed			Examination a week after treatment by Lane's method only
			1st day	2nd day	3rd day	
1	659	Hookworm, *Taenia*, *Heterodera*	*Taenia* segments	*Taenia* segments, 8 hookworms	Negative	No hookworm eggs
2	661	Hookworm	*Taenia* segments	Negative	2 hookworms	Negative
3	669	Hookworm, *Trichuris*	*Taenia* segments	Negative	Negative	No hookworm eggs
4	670	Hookworm, *Trichuris*, *Heterodera*	Negative	Negative	Negative	Hookworm
5	671	Hookworm, apparently very heavy, *Trichuris*, *Heterodera*	*Taenia* segments	1 hookworm	Negative	Hookworm
6	672	Hookworm, fairly heavy, *Heterodera*	Negative	1 hookworm	Negative	Negative
7	673	Hookworm, light, *Trichuris*, *Heterodera*	*Taenia* segments	Negative	Negative	No hookworm eggs
8	674	Hookworm, fairly heavy, *Heterodera*	Negative	Negative	Negative	No hookworm eggs
9	676	Hookworm, light, *Ascaris*	Negative	1 *Ascaris*	Negative	No hookworm eggs
10	679	Hookworm, *Trichuris*	Negative	Negative	Negative	No hookworm eggs

Batch 8.

These boys all said that they had intestinal worms. No preliminary investigation was carried out.
Treated (?) 5. x. 26. 3 c.c. CCl_4 followed at once by mag. sulph. oz. 1 in saturated solution.

No.	Ref'y no.	Worms passed			Faecal examination after treatment	
		1st day	2nd day	3rd day	After one week, by Lane's method only	After at least eight weeks. Whole stool
1	683	*Taenia* segments	*Taenia* segments	Negative	*Oxyuris*	Negative
2	685	Negative	Negative	Negative	*Ascaris*	*Taenia* segments
3	693	Negative	*Taenia* segments	Negative	Negative	Negative
4	702	Negative	Negative	Negative	Negative	Segments
5	709	1 hookworm	Negative	Negative	*Trichuris*, *Heterodera*	Negative
6	711	*Taenia* segments	1 hookworm	Negative	*Trichuris*	Negative
7	723	Negative	Negative	Negative	*Trichuris*	Negative
8	688	*Taenia* segments	*Taenia* strobila	Negative	*Ascaris*, *Heterodera*	Negative
9	695	*Taenia* strobila	*Taenia* segments	Negative	*Trichuris*	Negative
10	699	*Taenia* segments	*Taenia* segments, 1 hookworm	Negative	*Trichuris*	Negative
11	714	*Taenia* segments	*Taenia* segments	Negative	Negative	*Taenia* strobila
12	717	*Taenia* segments	*Taenia* strobila	Negative	*Trichuris*, *Heterodera*	Negative
13	722	Negative	*Taenia* strobila	Negative	*Trichuris*	Negative

Batch 9.

Treated 10. v. 27. A preliminary purgative was given and the boys were starved for eighteen hours before treatment.
Treatment. Ext. *Filicis Maris* dr. 1, followed an hour later by castor oil oz. ½.
After one week. No boy showed *Taenia* segments in his faeces on examination of a stool.

No.	Ref'y no.	Preliminary faecal examination	Worms passed			Whole stool examination on 14. x. 27
			1st day	2nd day	3rd day	
1	584	*Taenia* ova	9 gravid segments	Negative	2 fragments	Discharged from reformatory
2	618	*Taenia* ova	No stool	Strobila, apparently complete, no head	1 segment	Negative
3	660	*Taenia* and *Trichuris*	*Taenia* strobila, complete no head	Negative	Negative	Segments
4	665	*Taenia* ova	2 gravid segments	Negative	Negative	Segments
5	690	*Taenia* ova	17 mature segments	Negative	1 segment	Segments
6	621	*Taenia*, *Trichuris*, *Heterodera*	3 mature segments, two portions close to neck each 1 inch long	Negative	Negative	Negative
7	666	*Heterodera*, *Trichuris*, *Taenia*, *Strongyloides*	Small strobila, segments	Negative	Negative	Negative

KABETE REFORMATORY—*continued.*

Batch 10.

Thirty cases of Taeniasis extracted from the general helminthological investigation.
Most of the cases were only diagnosed on being treated with CCl_4 for Ancylostomiasis.
Treated at various times with doses of CCl_4 varying from 2 to 4 c.c.

No.	Ref'y no.	Preliminary faecal examination	Worms passed			Whole stool examinations	
			1st day	2nd day	3rd day	After one week	After at least eight weeks
1	505	Hookworm	*Taenia* segments	*Taenia* segments	Negative	Negative	Negative
2	518	Hookworm, heavy	*Taenia* segments	*Taenia* strobila	Negative	Hookworm	Negative
3	565	Hookworm	*Taenia* segments	*Taenia* strobila, 2 *Necator*	Negative	Negative	Negative
4	472	Hookworm, light	*Taenia* segments	*Taenia* strobila, 4 hookworms	Negative	Negative	Negative
5	516	Hookworm, light	Negative	*Taenia* segments, 4 hookworms	Negative	Negative	Negative
6	539	Hookworm, very light	*Taenia* segments	*Taenia* strobila, 1 hookworm	*Taenia* segments, 1 hookworm	Negative	Negative
7	579	Hookworm, *Trichuris*, very light, *Taenia*	*Taenia* segments	*Taenia* strobila, 2 hookworms, 1 *Oxyuris*	Negative	Hookworm	Negative
8	591	Negative	*Taenia* segments	Negative	Negative	Hookworm	Negative
9	513	Hookworm, *Taenia*	*Taenia* segments	Negative	Negative	Negative	Negative
10	558	Hookworm, fairly heavy, *Trichuris*	Negative	*Taenia* segments	Negative	*Trichuris*	Negative
11	582	Hookworm, light	Negative	*Taenia* segments	Negative	Negative	Negative
12	606	Hookworm, fairly heavy, *Trichuris*, *Heterodera*	*Taenia* segments	*Taenia* strobila, 11 hookworms, 1 *Oxyuris*	Negative	Hookworm, very light	Negative
13	613	Hookworm, heavy, *Trichuris*	*Taenia* segments	*Taenia* strobila, 18 hookworms	2 hookworms	Negative	Negative
14	614	Hookworm	Negative	*Taenia*, neck, head, 4 hookworms	*Taenia* head, 2 *Oxyuris*	Negative	Negative
15	616	Hookworm, light, *Taenia*	*Taenia* segments	Negative	Negative	Negative	Negative
16	620	Hookworm, light, *Trichuris*, *Heterodera*	*Taenia* segments	*Taenia* neck, 1 hookworm	3 hookworms, *Taenia* segments	*Trichuris*	Negative
17	624	Hookworm, *Heterodera*	*Taenia* segments	*Taenia* segments, 3 hookworms	Negative	Hookworm	Negative
18	625	Hookworm, light	*Taenia* segments	*Taenia* segments, 1 *Oxyuris*, 5 hookworms	*Taenia* segments, 1 hookworm	Negative	Negative
19	627	Hookworm, light, *Trichuris*	*Taenia* segments	*Taenia* segments	Negative	*Trichuris*, *Heterodera*	Negative
20	632	Hookworm, *Trichuris*	*Taenia* segments	*Taenia* strobila, 34 hookworms	Negative	*Heterodera*	Negative
21	641	Hookworm, *Trichuris*	*Taenia* segments	6 hookworms	Negative	*Trichuris*, *Heterodera*	Negative
22	644	Hookworm, light, *Heterodera*	Negative	*Taenia* segments	Negative	*Heterodera*	*Taenia* segments
23	648	Hookworm, *Heterodera*	Negative	*Taenia* segments, 2 hookworms	2 hookworms	*Heterodera*	Negative
24	650	*Taenia*, Hookworm, light, *Trichuris*, *Heterodera*	*Taenia* segments	*Taenia* segments	Negative	*Heterodera*	Negative
25	656	*Taenia*, Hookworm, light, *Heterodera*	*Taenia* segments	*Taenia* segments, and strobila, 1 hookworm	Negative	Hookworm, *Trichuris*, *Heterodera*	Negative
26	659	*Taenia*, Hookworm, *Heterodera*	*Taenia* segments	*Taenia* segments, 8 hookworms	Negative	Negative	Negative
27	661	Hookworm	*Taenia* segments	Negative	2 hookworms	Negative	Negative
28	669	Hookworm, *Trichuris*	*Taenia* segments	Negative	Negative	Negative	Negative
29	671	Hookworm, very heavy, *Heterodera*, *Trichuris*	*Taenia* segments	1 hookworm	Negative	Hookworm, *Trichuris*, *Heterodera*	Negative
30	673	Hookworm, light, *Trichuris*, *Heterodera*	*Taenia* segments	Negative	Negative	Negative	Negative

NAIROBI GAOL.

Batch 1.

All passed *Taenia* segments on 24. v. 27.
Admitted to Hospital 24. v. 27, starved till next day.
Treated 25. v. 27.
Treatment. CCl_4 dr. 1, followed at once by mag. sulph. oz. 1.

No.	Prison no.	Worms passed			Whole stools examined	
		1st day	2nd day	3rd day	One week	Eight weeks
1	D. 2570	Small strobila	Large strobila, 3 hookworms	Segments	Segments	Gravid segments
2	D. 1478	Small strobila	Large strobila	Segments	Negative	Gravid segments
3	D. 1473	Many segments	Large strobila	Negative	Negative	Gravid segments
4	D. 1952	Many segments	Strobila, partly digested	Strobila, partly digested	Negative	3. x. 27. Negative
5	D. 2140	Small strobila	Many segments	Strobila and neck, partly digested	Negative	3. x. 27. Negative
6	D. 1174	Segments	Many segments	Segments and neck, partly digested	Negative	Discharged from gaol
7	D. 1337	Segments	Large strobila, many segments, no neck	Large strobila and neck	Negative	3. x. 27. Negative
8	D. 1081	Segments	Negative	Negative	Segments	Chain of segment
9	D. 1335	Segments	Long strobila and neck, 10 *Oxyuris*	Segments	Segments	Gravid segments
10	D. 465	Short strobila	Short strobila and neck, 2 *Oxyuris*	Long strobila, no neck	Segments	Discharged from gaol
11	D. 1080	Negative	Long strobila and neck	Strobila, partly digested	Segments	Chain of segments
12	D. 3536	Negative	Long strobila and neck, 61 *Oxyuris*	Negative	1 *Oxyuris*	3. x. 27. Negative

Batch 2.

All passed *Taenia* segments on 14. vi. 27.
Admitted to Hospital mid-day 14. vi. 27, starved until next day.
Treated 15. vi. 27. CCl_4 dr. 1, followed at once by mag. sulph. oz. 3.

No.	Prison no.	Worms passed			Whole stools examined	
		1st day	2nd day	3rd day	One week	Eight weeks
1	D. 2605	Strobila and neck	Strobila and neck	Strobila and neck, much digested	Strobila and neck, much digested	Small strobila
2	C. 3120	Segments	Strobila and neck, partly digested	1 segment	Negative	3. x. 27. Negative
3	D. 2427	Segments	Chain of mature segments	Chain of immature segments	Negative	Gravid segments
4	D. 1808	Negative	Strobila and neck, 9 *Oxyuris*, 1 hookworm	Segments, 1 *Oxyuris*, 1 *Trichuris*	1 much digested fragment	Gravid segments
5	D. 1038	Strobila and head	Segments	Many fragments, much digested	Negative	Discharged from gaol
6	D. 623	Segments	Chain of mature segments	Negative	Negative	Gravid segments
7	D. 190	Segments	Long strobila to neck	Negative	Negative	5. x. 27. Negative
8	D. 295	Negative	Chain of gravid segments	Negative	Short strobila near neck, fragments	5. x. 27. Negative
9	C. 886	Segments	Strobila and neck	Gravid segments	Negative	Gravid segments
10	D. 2606	Segments	Strobila and neck	Gravid segments	Negative	Gravid segments
11	D. 1898	Segments	Strobila and neck	Gravid segments	Negative	Gravid segments
12	D. 1699	Segments	Strobila and neck	Gravid segments	Negative	Gravid segments

NAIROBI GAOL—*continued*.

Batch 3.

All passed segments of *Taenia* on 28. vi. 27.
Admitted to Hospital at mid-day on 28. vi. 27, and starved until next day.
Treated 29. vi. 27. CCl_4 dr. 1, oil of chenopodium mm. 20, followed at once by mag. sulph. oz. 3.

No.	Prison no.	Worms passed: 1st day	2nd day	3rd day	Whole stools examined: One week	Eight weeks
1	D. 2241	Segments	Large strobila, 4 hookworms	Gravid segments, neck, partly digested	Segments	Gravid segments
2	D. 2673	Segments	Large strobila	Gravid segments	Segments	Gravid segments
3	D. 1439	Segments	Large strobila	Chain of mature segments	Segments	7. x. 27. Negative
4	D. 1443	Segments	Large strobila	Segments	Segments	7. x. 27. Negative
5	D. 2745	Segments	Large strobila, 5 *Oxyuris*, 1 *Ascaris*, 6 hookworms	Strobila	Segments	Gravid segments
6	D. 2906	Segments	Small strobila, segments	Chain of segments	Segments	7. x. 27. Negative
7	D. 2868	Segments	Large strobila	Large strobila and neck	Segments	Gravid segments
8	D. 1353	Segments	Large strobila, neck, 2 hookworms	Segments	Negative	Gravid segments
9	D. 2869	Chain of mature segments	Large strobila, neck, ? head	Chain of segments	Negative	7. x. 27. Negative
10	D. 2049	Segments	Large strobila	Segments	Negative	Gravid segments
11	D. 1711	Segments	Segments	Large strobila, neck, 3 *Oxyuris*, 1 hookworm	Negative	7. x. 27. Negative
12	D. 2592	Segments	Large strobila	Negative	Negative	7. x. 27. Negative

Batch 4.

All passed *Taenia* segments on 9. viii. 27.
Admitted to Hospital 9. viii. 27, mid-day, starved until next day.
Treated 10. viii. 27. CCl_4 dr. 1, oil of chenopodium mm. 20, followed at once by mag. sulph. oz. 3.

No.	Prison no.	Worms passed: 1st day	2nd day	3rd day	Whole stools examined: One week	Eight weeks
1	D. 1193	Strobila near neck, much digested	Many segments and digested fragments, 1 *Trichuris*	Negative	Short lengths of much digested strobila	Discharged from gaol
2	D. 1044	Strobila and neck, much digested	Strobila, 2 heads, 11 *Oxyuris*	Short strobila	Negative	1 segment
3	D. 1042	Chain of mature segments	Strobila and neck	Strobila, much digested	Negative	7. x. 27. Negative
4	D. 31	Negative	Negative	Negative	Negative	7. x. 27. Negative
5	D. 2783	Many segments	Strobila, neck, head, 1 *Oxyuris*	1 *Ascaris*	Negative	7. x. 27. Negative
6	D. 1975	Many segments	Strobila and neck	Negative	Negative	7. x. 27. Negative
7	D. 2318	Many segments	Strobila and neck	Strobila, much digested	Long, partly digested, strobila	1 segment
8	D. 2933	Many segments	Strobila and neck	1 *Ascaris*, 5 hookworms	Negative	Discharged from gaol
9	D. 1191	Many segments, ? head	Strobila and neck	Negative	Negative	7. x. 27. Negative
10	D. 2595	2 segments	Strobila and neck	2 hookworms	Negative	7. x. 27. Negative

NAIROBI GAOL—*continued.*

Batch 5.

All passed *Taenia* segments on 15. viii. 27.
Admitted to Hospital at mid-day on 15. viii. 27, starved until next day.
Treated 17. viii. 27.
Treatment. CCl_4 dr. 1, oil of chenopodium mm. 20, followed at once by mag. sulph. oz. 3.

No.	Prison no.	Worms passed			Whole stool examined	
		1st day	2nd day	3rd day	One week	Eight weeks
1	D. 716	Many segments	Large strobila	Gravid segments	Negative	12. x. 27. Negative
2	D. 164	Short chain of immature segments	Large strobila, head, 5 hookworms, 1 *Oxyuris*	1 head, 8 hookworms	1 hookworm	12. x. 27. Negative
3	D. 1622	Many segments	Large strobila	Large strobila and neck	Negative	12. x. 27. Negative
4	D. 1733	Many segments	Large strobila	Strobila and neck	Negative	12. x. 27. Negative
5	D. 2251	Many segments	Large strobila	Gravid segments	2 gravid segments	12. x. 27. Negative
6	D. 2612	Many segments	Large strobila, neck	Gravid segments, neck	Negative	Chain of gravid segments
7	Kibligan	Large strobila	Large strobila, 4 heads, 1 *Oxyuris*	Negative	Negative	12. x. 27. Negative
8	D. 2953	No stool	Gravid segments, short strobila, much digested fragments, neck	Gravid segments, short strobila, much digested fragments, neck	Negative	1 segment
9	D. 1336	Negative	Short strobila, much digested fragments	Short strobila, much digested fragments	Negative	12. x. 27. Negative
10	D. 2757	Segments	Strobila, 2 heads	Many gravid segments, fragments, 1 head	Negative	12. x. 27. Negative
11	D. 1785	Segments	Strobila, 3 heads	3 short strobilae, 2 feet, 1 head	Negative	12. x. 27. Negative
12	D. 495	Segments	Strobila	3 short strobilae, gravid segments, 3 heads	Negative	12. x. 27. Negative

Batch 6.

All passed *Taenia* segments on 22. viii. 27.
Blood taken for calcium estimation on 23. viii. 27.
Admitted to Hospital 23. viii. 27, mid-day, starved till next day.
Treated 24. viii. 27.
Treatment. CCl_4 dr. 1, oil chenopodium mm. 20, followed immediately by mag. sulph. oz. 3.

No.	Prison no.	Worms passed			Whole stools examined	
		1st day	2nd day	3rd day	One week	Eight weeks
1	D. 1637	2 short strobilae	Strobila with neck	Segments, 1 hookworm	No stool	Discharged from gaol
2	D. 3072	Segments, 1 *Oxyuris*	Many segments, 9 *Ascaris*, 7 hookworms, 2 *Oxyuris*	Segments, 8 hookworms, 13 *Ascaris*	Negative	Segments
3	D. 2641	Segments, 1 *Oxyuris*	Many segments	Short strobila, no neck	Many segments, partly digested	Segments
4	D. 1698	Many segments	Large strobila, 2 necks, 1 head, 2 hookworms	Long strobila with neck segments	Negative	Segments
5	D. 2698	Segments	Strobila, 2 necks, 13 hookworms	Segments	Negative	Negative
6	D. 1185	Segments	Segments	Segments	Negative	Discharged from gaol
7	D. 1694	Segments	Short strobila, many segments	Long strobila with neck segments	Negative	Negative
8	D. 620	Segments	Much material, very digested	Segments	Negative	Negative
9	D. 1713	Many segments	Strobila and neck	Segments	Negative	Negative
10	D. 2667	Many segments	Large strobila	Negative	Negative	Discharged from gaol
11	D. 1344	Negative, very small stool	Strobila and neck	Segments	Negative	Negative
12	D. 2433	Segments	Strobila and neck	Segments	Negative	Negative

NAIROBI GAOL—*continued.*

Batch 7.

All passed segments of *Taenia* on 30. viii. 27.
Admitted to Hospital on 30. viii. 27, castor oil given and then fluid diet until treated.
Treated 1. ix. 27.
Treatment. CCl_4 dr. 1, oil of chenopodium mm. 20, followed at once by mag. sulph. oz. 3.

No.	Prison no.	Worms passed			Whole stools examined	
		1st day	2nd day	3rd day	One week	Eight weeks
1	D. 1395	Segments	Strobila and neck	No stool	Negative	Segments
2	D. 1345	Short chain of immature segments	Strobila, 2 heads	A few digested fragments	2 segments	Discharged from gaol
3	D. 1846	Segments, 2 *Oxyuris*	Segments, 1 *Oxyuris*	No stool	2 segments, 2 hookworms	Segments
4	D. 1782	Segments, short strobila, 1 hookworm	Strobila, 2 heads	Much partly digested material	1 segment	Segments
5	D. 2383	Many segments	Strobila and neck, 1 *Oxyuris*	Much partly digested material	1 segment	Segments
6	D. 2571	Many segments	Strobila, 1 head	Negative	2 segments	Segments
7	D. 2362	Many segments, 1 *Oxyuris*	Strobila, 2 *Oxyuris*	Negative	3 segments	Segments
8	D. 1626	Many segments	Strobila, 1 head	A few segments, much partly digested material	Negative	Segments
9	D. 1809	No stool	Strobila and neck	No stool	2 segments	Segments
10	D. 2787	Many segments	Large strobila	Much partly digested material	Negative	Segments
11	D. 2805	Many segments	2 complete strobilae with necks, 1 head, 1 hook worm	Negative	2 segments	Segments
12	D. 3127	Segments, 31 *Oxyuris*	Short chains of mature segments	Segments, partly digested material	Negative	Segments

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(*MS. received for publication* 6. iii. 1928.—Ed.)

FURTHER EXPERIMENTS ON THE ACTION OF EMETINE IN CULTURES OF *ENTAMOEBA HISTOLYTICA*.

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In 1926 two of us[1] published the results of a long series of experiments on the toxic action of the alkaloids of ipecacuanha in cultures of several species of entozoic amoebae. These experiments led us to definite conclusions regarding the differential susceptibility of the various species of amoebae studied, and the relative potency of the several alkaloids employed. They also showed clearly that the full specific action of emetine, on susceptible amoebae, is only disclosed if the alkaloid is allowed to act for a sufficient time (two or three days).

In all these experiments the amoebae were cultivated in a medium which was somewhat complex, but which was then believed to be the simplest available. It consisted partly of solid (inspissated fresh horse-serum) and partly of liquid (egg-white diluted with Ringer's fluid). To the liquid a small amount of sterile solid rice-starch was added just before use, and—except in the case of the control cultures—a known amount of a sterilized solution of the alkaloid to be studied. For purposes of comparison the original concentration of the alkaloid in the fluid part of the medium was recorded, though it was pointed out that an unknown amount of this added alkaloid would pass into the solid, so that the concentrations given were not absolute. But as medium of uniform composition was employed, and all tubes were handled in precisely the same way, we considered that any variation in alkaloidal content would be proportionate in all cultures, so that it would be permissible to compare the figures among themselves, as relatively true, whilst recognizing that they had no absolute value.

Other observers (Kofoid and Wagener, 1925; Vogel, 1927; Sautet, 1927) have now published other work along somewhat similar lines, and some confusion has arisen through the wide divergence of the figures which have been recorded as representing the lethal concentration of emetine—and also of other drugs—for *E. histolytica*. Sautet even considers the discrepancies to be so great as to make it doubtful whether this method of testing drugs is valid. With regard to our own records, however, we would point out that he

[1] Dobell and Laidlaw (1926).

has ignored[1] the explicit limitations placed upon our published figures; while Vogel likewise has mistaken our comparative concentrations for absolute values.

The publications just mentioned show great divergence in experimental technique. To note only three points of prime importance: (1) the duration of the exposure of the amoebae to emetine, or other drugs, varies in the different sets of experiments; (2) the criterion adopted to indicate a definitely toxic effect is equally variable; (3) the culture-medium employed by the several workers is not the same. As all these factors vary so widely, we feel that it is impossible to compare the results of different workers; and we consider that Sautet is therefore prematurely pessimistic in his estimate of the value of tests of amoebicidal activity by cultural methods.

However that may be, there is no doubt that confusion exists; and we therefore considered it desirable to make further experiments in order to elucidate some of the discrepancies, and also to define, if possible, the lethal concentration of emetine for *E. histolytica* more closely.

Our new work falls naturally into two sections—(1) an assay of the distribution of emetine after addition to the somewhat complex culture-media used by most workers; and (2) a determination of the lethal concentration of emetine for *E. histolytica* in the simplest culture-medium possible.

(1) The distribution of emetine[2] in media composed of solid and liquid.

The importance of the kind of culture-medium used was shown clearly by the experience of one of us (A. B.), who desired to determine the susceptibility of a certain strain of *E. histolytica* to emetine. The medium of Boeck and Drbohlav was first employed, and the strain appeared to be resistant: but repetition of the tests in the medium of Dobell and Laidlaw showed that this strain was really just as sensitive as those usually encountered. These observations show that results obtained by the use of different media are not comparable. Sautet, however, employed Boeck and Drbohlav's medium; Kofoid and Wagener used their own modification of this; and Vogel used two of the later modifications introduced by Drbohlav.

It is obviously necessary, before attempting to draw any conclusions, to ascertain how the emetine is distributed in such different media; and we

[1] The primary object of Sautet's work was, apparently, to discover a difference, in response to emetine, between *E. histolytica* and "*E. dispar.*" In this he failed: but we are not surprised, as we regard these species as identical. If he had read our papers (1926, 1926 *a*) more carefully, he would have seen that we had already recorded that there is no difference between *E. histolytica* and "*E. dispar*" in their reaction to emetine in cultures: for our *Strain D*—from its history and behaviour—would be called *E. histolytica* by Brumpt and Sautet, and our *Strain F.* would be regarded by them as "*E. dispar*" (though we consider it to be undoubtedly *E. histolytica*). Sautet's observations confirm our view that "*E. dispar*" differs in no way from *E. histolytica.* (C.D., P. P. L.)

[2] The salt of emetine used in all our experiments has been the pure hydrochloride, manufactured by Burroughs, Wellcome and Co.

decided to study this problem in the two chief types of medium hitherto employed—that of Boeck and Drbohlav (solid egg with liquid serum) and that of Dobell and Laidlaw (solid serum with liquid egg-white). As these two media consist of different solids and liquids, it appeared theoretically improbable that the partition of emetine between solid and liquid would be identical in both. The amount of emetine taken up from the Ringer-serum mixture by coagulated whole egg (Boeck-Drbohlav medium) would probably be different from that abstracted by inspissated horse-serum from Ringer-eggwhite (Dobell-Laidlaw medium). The apparent inefficiency of emetine in Boeck-Drbohlav medium—as compared with its relative efficiency in that of Dobell and Laidlaw—might therefore be due to the coagulated egg abstracting more emetine from the fluid, so that the concentration of alkaloid bathing the amoebae—which we must regard as the effective concentration—would be low in Boeck-Drbohlav medium, but relatively high in that of Dobell and Laidlaw.

Such speculations, by themselves, have small weight; but we have been able to show by chemical methods that they can be justified, and that the amount of emetine deviated by the solid part of such culture-media varies with the nature of the solid and also with the hydrogen-ion concentration. It is therefore inadmissible to compare the figures for lethal concentration secured by the use of one medium, with those obtained when employing another of quite different composition.

The estimation of emetine.—So far as we are aware, there is no simple or generally recognized method for the estimation of small quantities of emetine, and we have thus been forced to adopt an indirect method depending on the turbidity which develops when Mayer's reagent is added to the faintly acid solution of any alkaloid. For our purpose it was necessary to separate the emetine from all other substances which would give a precipitate with this reagent. It might have been expected that proteins and extractives in the culture-medium would interfere with the reaction, but we found that the proteins alone caused trouble. The extractives, and even the bases formed by the bacteria in our cultures, were present in concentrations too small to cause any visible turbidity with the alkaloidal reagent.

Separation of the emetine from the proteins did not prove easy. Attempts to remove the proteins by heat-coagulation, or by ammonium sulphate and heat, were unsuccessful; for the protein coagulum invariably carried down a large proportion of the added emetine. Precipitation of the protein by means of salicyl-sulphonic acid was tried, as this reagent was found to give no precipitate with emetine and yet precipitated the protein in a strongly acid solution: but this method again led to great loss of alkaloid. The only method which gave us reliable results, and which we ultimately adopted, was to pour the liquid part of the culture-medium into ten volumes of absolute alcohol, mix thoroughly, and boil. The whole of the protein could then be filtered off in a Büchner funnel at the water pump. If the coagulum was then washed

with alcohol, the whole of the emetine was found in the filtrate and washings. The alcoholic solution was evaporated to dryness, under negative pressure, and the remaining solid treated with a known volume of 0·1 per cent. sulphuric acid, which extracted the alkaloid and the simple substances, while the lipoids remained undissolved. The acid solution was filtered, and—whenever practicable—a dilution of this solution was made for comparison with the standard dilutions of emetine. Serial dilutions of the standard and the unknown having been prepared in tubes of approximately the same bore, the same proportion of Mayer's reagent was added to each tube and time allowed for maximum turbidity to develop. The unknown solution was then matched nephelometrically against the standards as accurately as possible, and the amount of emetine in it calculated from the nearest match.

The chief difficulty—separation of emetine from protein—was surmounted in the way described; but there is a minor difficulty which may become serious in the case of weak solutions of alkaloid. In the technique just outlined, the salts and other simple substances in the medium are still present when the alkaloid is precipitated by the Mayer's reagent. These substances, though they give no turbidity with this reagent, influence the character of the precipitated emetine-mercuric-iodide complex. For any accurate nephelometric comparison to be made, however, the state of aggregation of the particles must be the same in the standard and in the unknown dilutions: and consequently, we consider our estimates most exact when the emetine was present in fairly large quantities, and simple salts in minimal amount.

Accurate nephelometric estimation really demands isolation of the alkaloid in a pure state as a preliminary to the actual test. Our efforts in this direction were disappointing. Extraction of the alkaloid by ether from faintly alkaline solution and re-extraction of the alkaloid from the ether by acids, did not yield any better results. We found that the peroxides usually present in ether decomposed the Mayer's reagent and made nephelometric comparisons impossible. Moreover, we soon discovered that our imperfect method gave results which were decisive, and clearly proved that the different types of medium deviated quite different amounts of emetine.

Experimental findings. All our estimations of emetine were made with two different media: (1) that of Boeck and Drbohlav, and (2) that of Dobell and Laidlaw. The culture-tubes used were taken at random from different batches, and it is thus probable that trivial variations in composition occurred from time to time. Sterile solutions of emetine were added, with ordinary aseptic precautions, in equal amounts to every tube; and all were then incubated at 37° C., for varying periods of time, and the emetine content of the liquid constituent afterwards assayed in the manner described above. The tubes were always dealt with in pairs—one tube of each type of medium—and the whole of the liquid (5 c.c.) was employed for an estimation. No attempt was made to determine the emetine content of the solid constituent.

Sufficient emetine was first added to produce a concentration of 1 : 1000

in the liquid in each type of medium, and the alkaloidal content then determined after ten minutes' incubation. The whole of the emetine was recovered after this short period. When the tubes were incubated for 24 hours, however, the result was very different. A large proportion of the added alkaloid disappeared from the liquid. The loss was greater after two days, and still greater after four. The results are summarized in Table I[1].

Table I.

Medium	Original concentration of emetine	Concentration found after 1 day	2 days	4 days
HSre	1 : 1000	1 : 5,500	—	—
HSre	1 : 1000	1 : 3,000	—	—
HSre	1 : 1000	1 : 3,500	—	—
HSre	1 : 1000	1 : 3,500	1 : 9,000	—
HSre	1 : 1000	1 : 3,000	1 : 8,000	1 : 12,000
Ehs	1 : 1000	1 : 6,500	1 : 11,000	1 : 24,000
Ehs	1 : 1000	1 : 6,000	—	—
Ehs	1 : 1000	1 : 5,000	—	—
Ehs	1 : 1000	1 : 10,000	—	—
Ehs	1 : 1000	1 : 10,000	—	—

It will be observed that the loss of emetine from the fluid is always much greater in the tubes containing solid egg. It is, on the whole, about twice that which occurs in the medium with a solid horse-serum basis. Further, the longer the tubes are incubated, the greater the apparent loss of emetine; or, to put it in another way, there is no evidence of the establishment of an equilibrium between the proportion of emetine in the solid and that in the liquid parts of the medium. The addition of solid rice-starch to the liquid was found to be without influence on the final results.

The same type of experiment was repeated with one-tenth the initial concentration of emetine in the fluid, and substantially the same answer was obtained. (See Table II.)

Table II.

Medium	Original concentration	Concentration found after 1 day	2 days	4 days
HSre	1 : 10,000	1 : 30,000	1 : 60,000	1 : 80,000
Ehs	1 : 10,000	1 : 50,000	1 : 100,000	1 : 120,000

Solid egg thus abstracts more emetine from the fluid than solid serum does during an equal time of incubation.

A few experiments were then made with concentrations of emetine so small as to be only just lethal for most cultures of *E. histolytica*. (See Table III.) Exact estimation of such minute amounts is not always possible, and it is thus doubtful how far the figures obtained are trustworthy. (Cf. p. 210.) Nevertheless, it will be observed that once more the tubes containing solid egg lost more emetine than those with solid horse-serum.

[1] In this and following tables HS = solid horse-serum; re = Ringer's fluid and egg-white; E = solid whole egg; hs = horse-serum diluted with Ringer's fluid (1 : 8). See Dobell and Laidlaw (1926 *a*), p. 294.

Table III.

Medium	Original concentration	Concentration after 4 days
HSre	1 : 40,000	1 : 220,000
HSre	1 : 50,000	1 : 240,000
Ehs	1 : 40,000	1 : 300,000
Ehs	1 : 50,000	1 : 300,000

At every concentration, therefore, the loss from the egg-tubes is greater, and in all tubes the disappearance of emetine from the liquid part of the medium is continuous throughout the period studied—a period which is ample to disclose the full amoebicidal activity of the alkaloid.

This absence of an equilibrium was again well illustrated by some tubes of Boeck-Drbohlav medium which had been made up to contain emetine 1 : 6000, incubated overnight (to test their sterility), and then kept at room-temperature. At the end of five weeks two tubes were taken and the emetine content of the liquid estimated. Instead of the original 1 : 6000, they were found to contain emetine 1 : 32,500 and 1 : 35,000. A third tube was then incubated for twenty-four hours, when its emetine content was found to have fallen to 1 : 60,000. Similar results were obtained when tubes were incubated and kept in the cold for shorter periods of time.

Two experiments with *iso*emetine showed that this alkaloid behaved in a similar manner, and disappeared from the liquid over coagulated egg more rapidly than from the liquid over inspissated serum.

In the emetine estimations so far considered the hydrogen-ion concentration of the medium has been ignored. Careful handling of the tubes insured their sterility throughout; but when they are actually used as culture-medium the reaction of the liquid changes, owing to the growth of bacteria and amoebae and the accumulation of their metabolic products. It was necessary, therefore, to ascertain whether variation of hydrogen-ion concentration influences the phenomena just described.

Three tubes of each type of medium were taken, and sufficient emetine added to the liquid to make a 1 : 1000 solution. To the first tube of each group 0·5 c.c. of Ringer's fluid was added; to the second, 0·5 c.c. of $N/10$ caustic soda; and to the third, 0·5 c.c. of $N/10$ hydrochloric acid. The pH of the fluid was determined on one drop withdrawn from each tube, and all six were then incubated for 24 hours at 37° C. At the end of this time the pH of the fluid was redetermined, again on a single drop, and the emetine content of the whole of the rest of the fluid estimated in the usual manner. The results are given in Table IV.

It will be observed that the initial large alteration in reaction of the liquid—brought about by the addition of acid or alkali—becomes greatly reduced on incubation for 24 hours, owing to the effective buffering action[1] of the denaturated protein forming the solid portion of the medium: nevertheless, it

[1] Cf. Dobell and Laidlaw (1926 *a*), p. 293.

Table IV.

Medium	Addition	Original		After incubation	
		*p*H	Emetine content	*p*H	Emetine content
HSre	0·5 c.c. Ringer's fluid	7·7	1 : 1000	7·8	1 : 3000
HSre	0·5 c.c. *N*/10 NaOH	11·0	1 : 1000	8·0	1 : 4000
HSre	0·5 c.c. *N*/10 HCl	3·9	1 : 1000	6·8	1 : 1500
Ehs	0·5 c.c. Ringer's fluid	7·2	1 : 1000	7·4	1 : 6000
Ehs	0·5 c.c. *N*/10 NaOH	11·0	1 : 1000	7·8	1 : 7000
Ehs	0·5 c.c. *N*/10 HCl	3·9	1 : 1000	6·5	1 : 3000

will also be seen that the emetine content of the fluid in either medium is profoundly modified by a change in reaction. It is true that the induced change is here large, but it is a change within the range encountered in cultures of amoebae—particularly with strains in process of isolation.

These experiments, taken together, show (1) that the initial concentration of emetine in the liquid part of a culture-medium (of the solid-liquid type commonly employed for growing entozoic amoebae) may fall appreciably after the lapse of a few hours, and very considerably after several days of incubation; (2) that it is impossible to compare results obtained by the use of one medium with those secured with another of different composition. If one medium alone be used, and all tubes handled in precisely the same manner, the results have a comparative value. But even so, there is some risk of error; for the amount of emetine lost by the fluid and adsorbed by the solid varies with the hydrogen-ion concentration. This, in turn, will vary with the bacterial flora—at present inseparable from cultures of amoebae. The particular forms of bacteria present, their relative proportions, and their individual rates of growth, may all influence the result.

(2) THE POTENCY OF EMETINE IN DILUTE SERUM ALONE.

It is thus clear that a medium which contains a mass of coagulated protein is unsuitable for quantitative chemotherapeutic experiments. As all the media commonly employed for cultivating parasitic amoebae suffer from this drawback, we tried to secure a simpler medium; and we ultimately found it possible to cultivate various laboratory strains of *E. histolytica* in inactivated horse-serum diluted with Ringer's fluid (1 : 8), to which a little sterile rice-starch had been added. This medium is thus very similar to that employed by Barret and Smith (1924) for cultivating the amoebae of turtles; but successful results were only achieved with difficulty[1], and with strains previously established in other media.

When it was found possible to maintain flourishing cultures of *E. histolytica* in this simple medium[2], known quantities of emetine were added to a number

[1] Cf. Dobell and Laidlaw (1926 *a*), p. 293.

[2] All strains of amoebae used in our experiments survive in this medium for at least a week, and usually for ten days or a fortnight. Stock-cultures were generally transplanted once a week.

of cultures, and the amount present then estimated after incubation. This was done in order to exclude two possible fallacies: first, that the solid rice-starch might deviate the alkaloid; and secondly, that the bacteria in the cultures might destroy the emetine. The results are shown in Table V.

Table V.

Medium	Emetine concentration	
	Originally	After incubation at 37° C. for 2 days
Dilute horse-serum and starch	1 : 100,000	1 : 100,000
	1 : 100,000	1 : 100,000
	1 : 50,000	1 : 75,000
	1 : 50,000	1 : 60,000
	1 : 50,000	1 : 75,000
	1 : 50,000	1 : 100,000
	1 : 50,000	1 : 75,000

It will be evident that there was but little loss of alkaloid, except in one experiment where the amount recovered was only half the original. In the others the apparent loss lay within the expected error of the method of estimation. In any case it is clear that the emetine was not destroyed in an amount which would seriously invalidate the figure representing its original concentration.

We therefore carried out a further series of experiments to determine the toxicity of emetine on cultures of *E. histolytica* grown in this simplified medium. In all these experiments the medium used was that just described—sterile horse-serum, 1 part; Ringer's fluid, 8 parts; with a small quantity of sterile solid rice-starch. In our first trials the Ringer's fluid had the following composition:

Sodium chloride	...	...	0·90 gm.
Potassium chloride	...	...	0·02 gm.
Calcium chloride	...	...	0·02 gm.
Glass-distilled water	...	...	100·00 c.c.

Four different strains of *E. histolytica* (one human and three simian) were used:

(1) *E. histolytica* from man—the strain (*D.*) employed by Dobell and Laidlaw (1926) in previous chemotherapeutic experiments. It was originally isolated by Dr Drbohlav from a case of acute human amoebic dysentery, and has now been maintained by us in culture for over three years.

(2) Strain *K.* 28*C.* from *Macacus sinicus*—isolated and cultivated for 18 months by one of us (C. D.).

(3) Strain *N.C.*, from *Macacus nemestrinus*—cultivated (by C. D. and A. B.) for about 7 months.

(4) Strain *J.C.*, from *Macacus rhesus*—recently isolated (by A. B.) for the purpose of these experiments.

Before making any experiments with these strains they were all critically studied (microscopically, both fresh and in stained preparations) and proved

(by obtaining and hatching their cysts) to be unmixed with other species. We regard it as absolutely essential, in an inquiry of this sort, to work with strains of guaranteed purity.

Graduated doses of emetine in sterile solution—carefully weighed and measured—were added, with aseptic precautions, to tubes of the medium just described; and these were then incubated to make sure that they were not contaminated. They were then inoculated with a small and approximately equal amount of amoebae from the stock-cultures. After the tubes had been incubated at 37° C. for three or four days, a small quantity of the deposit at the bottom was examined under the microscope. As a rule this direct examination was decisive, but in doubtful cases subcultures were made and the result ascertained after three or four days' incubation. In every experiment a control tube (without emetine) was inoculated, and no experiment was considered to be of any value unless the control showed copious growth during an equal period of time. The results of our first series of experiments are shown in Table VI.

Table VI.

Action of emetine on E. histolytica *in liquid cultures* (*dilute serum + starch*).

Incubation period 4 days.

Concentration of emetine	Strain *D.* (man)		Strain *K.* 28*C.* (*M. sinicus*)		Strain *N.C.* (*M. nemestrinus*)	
	Grew	Died	Grew	Died	Grew	Died
1 in 50,000	0	2	0	2	0	1
1 in 100,000	0	1	0	1	—	—
1 in 200,000	0	1	—	—	—	—
1 in 300,000	0	1	0	1	0	1
1 in 400,000	0	2	0	2	1	1
1 in 500,000	0	3	1	2	1	2
1 in 600,000	0	1	0	1	1	0
1 in 750,000	0	2	1	1	2	0
1 in 1,000,000	2	1	1	2	3	0
(Controls) nil	4	0	4	0	3	0

(The double columns under each strain show the number of cultures in which growth or death occurred at the concentration of alkaloid indicated.)

The minimum lethal concentration of emetine here appears much lower than might be supposed from the results of work with complex media containing solid and liquid portions. But this agrees with the results of our chemical investigations, which showed clearly that the solid adsorbs a large proportion of the emetine from the liquid, and thus renders it ineffective.

Closer examination of the results reveals, however, that the end-point is not always sharp, but varies from strain to strain and even with the same strain. After most of the above experiments were completed it was discovered that the final *p*H of the cultures was variable, and that the more acid (those showing a lower *p*H) were more likely to contain living amoebae. In other words, in an acid environment the emetine appeared to be less efficient. For example, with strain *N.C.*, in one experiment a concentration of 1 part

in 400,000 failed to kill, while 1 in 500,000 sterilized the culture. In the first instance the final *p*H was found to be 6·0 and in the second 6·6.

It was decided, therefore, to try and stabilize the reaction by adding 0·2 per cent. of disodium hydrogen phosphate to the Ringer's fluid used for diluting the serum—the reaction being adjusted to *p*H = 7·2. The results of a series of similar experiments made with amoebae cultivated in this buffered medium are shown in Table VII, and it will be seen that they are on the whole more regular.

Table VII.

Action of emetine on E. histolytica *in liquid cultures (dilute serum + phosphate + starch).*

Incubation period 4 days.

Concentration of alkaloid	Strain *D.* (man)		Strain *K.* 28*C.* (*M. sinicus*)		Strain *J.C.* (*M. rhesus*)		Strain *N.C.* (*M. nemestrinus*)	
	Grew	Died	Grew	Died	Grew	Died	Grew	Died
1 in 500,000	0	2 (6·5)	0	1 (6·6)	0	2 (6·3)	0	1 (6·6)
1 in 750,000	0	2 (6·5)	0	1 (6·6)	—	—	0	1 (6·6)
1 in 1,000,000	0	3 (6·6)	0	2 (6·6)	0	2 (6·3)	1 (6·2)	1 (6·7)
1 in 2,000,000	0	1 (6·6)	0	1 (6·6)	—	—	—	—
1 in 5,000,000	0	1 (6·7)	0	1 (6·6)	0	2 (6·4)	1 (6·2)	1 (6·8)
1 in 10,000,000	1 (6·6)	0	1 (6·3)	0	2 (6·4)	0	1 (6·6)	1 (6·6)
Nil	4 (6·4)	0	3 (6·3)	0	2 (6·4)	0	4 (6·4)	0

(The double columns under each strain show the number of cultures in which growth or death occurred at the concentration of alkaloid indicated. The figures in parenthesis show the average *p*H of the liquid at the end of incubation.)

It will also be observed that emetine here proved more uniformly toxic in higher dilutions; for all concentrations up to and including 1 in 5,000,000 proved lethal—except in two experiments. In these (with strain *N.C.*) survival occurred at 1 in 1,000,000 and 1 in 5,000,000. But it seems significant that the final reaction of the medium was here more acid (*p*H = 6·2) than usual, in spite of the added phosphate. In a parallel experiment, when the final reaction of the medium was *p*H = 6·8, emetine 1 in 5,000,000 proved lethal for this strain, as for the others.

From these findings it is clear that emetine is extremely poisonous for *E. histolytica* under certain defined conditions. Provided that the alkaloid remains in solution, and that the solution does not become too acid, a concentration of 1 part in 5,000,000 is lethal within four days for all the strains we have studied.

In all these experiments the medium employed was simple but efficient, and consisted of liquid only—uncomplicated by admixture with coagulated protein; the strains of amoebae were pure (*i.e.*, unmixed with other species) and derived from four different sources; our criterion of toxicity was death of all amoebae (controlled, when necessary, by subcultures), while control-cultures grew luxuriantly during the same period; ample time (3 or 4 days) was always allowed for the emetine to exercise its full effect; and the hydrogen-ion concentration throughout was stabilized as far as possible. We therefore

feel justified in concluding that our final figures represent a fairly close approximation to the absolute lethal concentration of emetine for *Entamoeba histolytica* under artificial conditions.

DISCUSSION.

Our results prove that great caution must be exercised in assessing the value of an amoebicidal agent when tests are made with cultures alone. They also show clearly that the results of experiments performed by one observer cannot be compared with those of another unless the same culture-medium was employed by both and the whole of the work carried out in exactly the same way.

In all chemotherapeutic tests *in vitro* with culture-media which contain two constituents of different physical and chemical composition—such as those commonly employed for cultivating entozoic amoebae—it is necessary to remember, first, the effect produced by the partition of the added drug between the two constitutents; and secondly, the possible effect of reaction on this unequal distribution.

Our experiments (Tables I, II, and III) show clearly that the medium devised by Boeck and Drbohlav is quite unsuitable for chemotherapeutic tests with alkaloids. On incubation, a large but variable proportion of the emetine added to the serum passes into the coagulated egg; so that, although a known amount of alkaloid may have been added to a given culture, the actual concentration present in the liquid, and acting upon the amoebae, rapidly becomes unknown and uncertain. As the exact conditions of experiment cannot, therefore, be defined, such an experiment is almost worthless. Medium composed of solid serum and dilute egg-white (Dobell and Laidlaw) is better adapted for the purpose, since the differential partition of the alkaloid between solid and liquid is here not so unequal. Nevertheless, the results show that tests made with such medium have only a relative—not an absolute—significance, and even then only when they are made in exactly the same way. This point was noted when our earlier experiments were described (Dobell and Laidlaw, 1926); but our later work—and that published by others—makes it necessary to emphasize it once more.

In our present experiments we have attempted to eliminate the error inherent in the use of a solid-liquid medium by employing one composed of liquid only. In such a medium the added emetine—as we have shown—remains approximately constant in amount. The conditions of experiment can therefore be defined with some certainty, and the attempt made to determine absolute toxicity under definite conditions. We have made this attempt, and have found that emetine hydrochloride is extremely poisonous for *E. histolytica* in very high dilutions (1 : 5,000,000) in the neighbourhood of neutrality.

In such experiments the reaction of the medium is a factor of importance. With Boeck-Drbohlav and Dobell-Laidlaw media (*i.e.*, with media consisting of solid and liquid protein combinations), alteration of the initial *p*H of the

liquid constituent determines a differential distribution of the added alkaloid. When the liquid is rendered more acid, less emetine passes into the solid: when it is more alkaline, less emetine remains in solution. (Cf. Table IV.) But whenever amoebae and bacteria are cultivated in such media, the reaction changes continually: it never remains constant for long. Consequently, it is impossible to predict what will happen to any added alkaloid. We do not know, and cannot determine, how much of it will remain in solution, and so be able to act; nor what absolute concentration is necessary to kill all amoebae in a culture, in a given time, or to insure their survival during an equal period. All that can be said with certainty is that emetine, in any concentration, would probably be more amoebicidal in cultures of this sort which become *acid* than in those which develop alkalinity on incubation.

Our experiments with wholly liquid culture-media (Table VII) also show that the reaction of the medium is important: but they show too that an *alkaline*—not an acid—reaction favours the amoebicidal efficacy of emetine. This result is, perhaps, paradoxical. But it is easily intelligible if it be assumed that emetine *as a base* is the lethal agent. In an acid medium the greater solubility of the salts of emetine in the fluid constituent would tend to prevent the base from being taken up by the amoebae. Our results, in fact, recall those of Gros (1910, 1912), who showed that the efficacy of local anaesthetic alkaloids increases when they are applied as the salts of weak acids, and diminishes when they are administered as salts of strong acids. This point has recently been restudied by Trevan and Boock (1927) in considerable detail, and they have shown that the evidence indicates that the anaesthetic agent is the free base; so that with a rising *p*H (increasing alkalinity) the efficiency of local anaesthetic alkaloids rapidly rises also. We have not been able, in our experiments with emetine, to control the reaction of the cultures as exactly as we should have liked, in order to establish this hypothesis on a firm foundation; but we regard it as significant that the exceptions to our usual results were always associated with an unusually acid reaction of the culture-medium.

With simple (*i.e.*, liquid—not solid-liquid) media, it is probable that the efficiency of alkaloids, in general, will rise with increasing alkalinity; but it by no means follows that the efficiency of an acidic amoebicidal agent will increase in the same manner. Indeed, it is more probable—on theoretical grounds—that the opposite will hold for acidic substances.

With a complex medium composed of solid and liquid, the effect of reaction is, in reality, doubly complicated; for the increasing alkalinity, which raises the efficiency of the alkaloid as a drug, also, upon occasion, causes a greater deviation of base from the liquid into the solid constituent, and thus throws a considerable amount of the alkaloid—present initially—out of action. It is impossible to ascertain the real state of affairs in a medium of this type under varying experimental conditions, or to forecast the results which may attend its employment.

At present we cannot accurately translate our test-tube experiments into terms of practical therapeutics. We have found that emetine is extremely toxic to *E. histolytica*, but that its toxicity may be counteracted by the presence of colloidal substances which adsorb it and so render it inactive, and by variations of hydrogen-ion concentration which profoundly modify its potency. When emetine is administered to a man suffering from amoebic dysentery, it is obvious that many factors may divert it from its desired destination—the parasites in his bowel. It appears highly probable that only a small proportion of the emetine so administered—by whatever route—ever reaches the lumen of the large intestine; and of that amount some at least must be adsorbed by the food-detritus and intestinal mucus. Our results cannot, therefore, be applied directly to therapeutics; but they do appear to us to show, more clearly than ever before, that the mode of action of emetine, upon the parasite of amoebiasis in man, is direct. Under defined conditions *in vitro*, emetine is extraordinarily toxic to *E. histolytica*—to an extent unparalleled, so far as we are aware, by any other drug: and it is difficult to believe that this extreme toxicity is altogether uncorrelated with the specific curative action of the same alkaloid when administered to an infected human being.

CONCLUSIONS.

1. When emetine is added to complex culture-media containing solid and liquid portions it becomes unequally distributed between the two constituents.

2. The distribution between the solid and liquid varies with (*a*) the nature of the solid, (*b*) the reaction of the system, and (*c*) the time.

3. An erroneous idea of the absolute toxicity of emetine for *E. histolytica* is obtained from a consideration of the results of tests with such media (*e.g.* the egg-serum medium of Boeck and Drbohlav).

4. With a simple (liquid) medium it has been shown that a solution of emetine 1 in 5,000,000 is lethal for all amoebae (*E. histolytica*—4 strains) *in vitro* within 4 days, provided that the medium does not become too acid.

5. This great potency of emetine *in vitro* may be altered by a comparatively small variation in the reaction of the culture-medium.

6. The results confirm the view that the therapeutic efficacy of emetine in human amoebic dysentery is probably due to the direct toxic action of the alkaloid upon the amoeba.

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(*MS. received for publication* 7. iv. 1928.—Ed.)

THE MALLOPHAGAN FAMILY MENOPONIDAE.

PART III[1].

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(With 3 Text-figures.)

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9. *Trinoton anserinum* (Fabricius).

7. **Myrsidea victrix** Waterston.

Material examined. A male and a female from *Ramphastos brevicarinatus*, Barro Colorado Island, Panama Canal Zone, collected by Mr J. Van Tyne of the University of Michigan, through whose kindness I have been enabled to examine them. The species was originally described from "probably *Ramphastos tocard*" (which is *R. brevicarinatus*) from Colombia. My material agrees with the original description and is probably correctly identified, although, as will be further considered, another species of the same genus occurs upon toucans.

Female (Fig. 7 *A*). A rather robust form, but with only slight pigmentation. *Head* about one and a half times wider than long, with the temples very prominent, widest just behind the eyes. Lateral margins (Fig. 7 *E*) entirely without either a slit or a notch in front of the eye. Antennary fossa (Fig. 7 *F*) very shallow, backed up only by a very narrow sclerotic and pigmented area. Pharyngeal sclerites and glands present. Gular region with a faintly indicated plate which bears only a few setae. Antennae (Fig. 7 *C*) four-segmented.

Prothorax quite large and broad, with narrow wings; sternum with a distinct plate which bears at the most a couple of small setae. *Mesonotum* very distinctly developed and nearly half as long as the pronotum; mesosternum with a distinct plate that at the most bears only a couple of small setae. *Metanotum* slightly longer than the pronotum, with several stout setae at the lateral angles and a few slender setae along the posterior border; metasternum a large, distinct, somewhat shield-shaped piece with a few small setae on its anterior portion. *Legs* of ordinary form, the posterior femora with a patch of quite stout setae on the ventral face.

[1] Part II appeared in *Parasitology* **18**, 1.

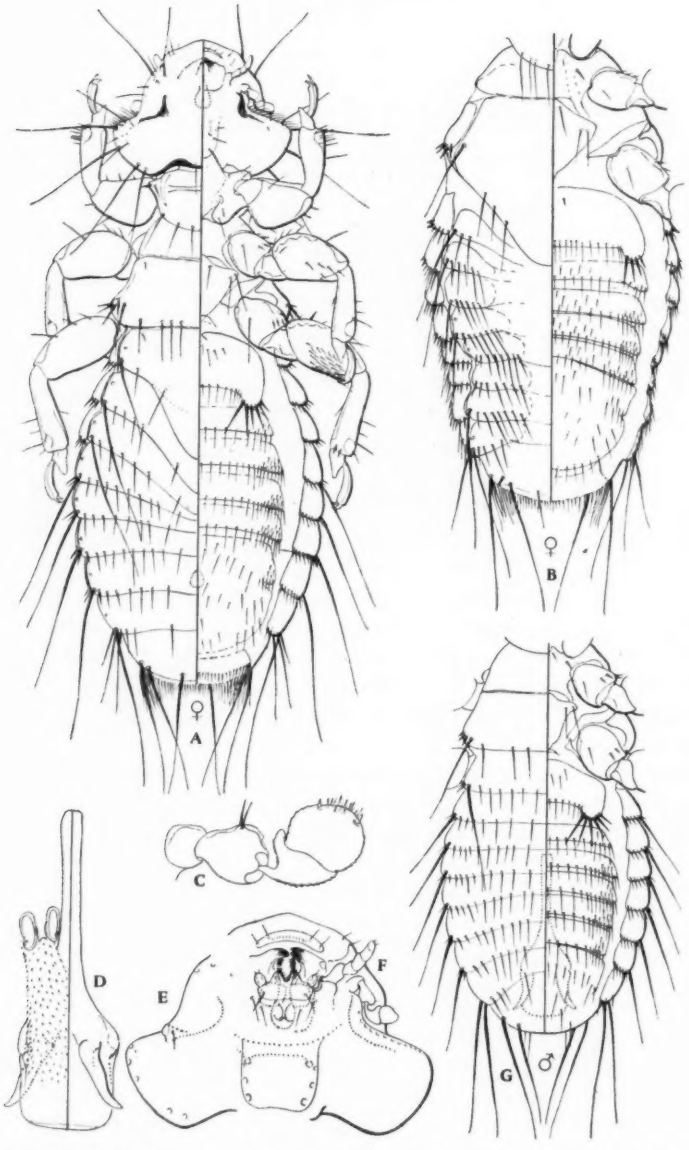

Fig. 7. *Myrsidea victrix* Waterston. *A*, female; *C*, antenna; *D*, genitalia of male; *E*, dorsal aspect of lateral margin of head; *F*, portion of ventral aspect of head; *G*, thorax and abdomen of male. *Myrsidea extranea* (Carriker). *B*, thorax and abdomen of female.

Abdomen with the plates quite well defined, the pleural plates distinctly separated from the tergites, each pleural plate with a row of small, thorn-like setae along its posterior border. Tergal plates more strongly pigmented at the lateral margins than in the centre. First tergal plate much enlarged and produced posteriorly, nearly to the posterior margin of the third segment, terminating in a broadly rounded point. The second to fourth tergites are consequently also displaced and forced posteriorly in their centre parts. The remaining tergites are normal. Chaetotaxy as indicated in the figure.

On the ventral side, the first sternite is greatly reduced and the second very much enlarged, its posterior lateral angles produced and bearing a cluster of six heavy setae. The third to seventh sternites show a tendency toward the development of a slight brush of small setae at the posterior lateral angles. Seventh and eighth sternites fused into a single large genital plate. The apical plates, both dorsally and ventrally terminate in a fringe of fine setae.

Male (Fig. 7 *G*). In the characters of head, thorax, legs and venter of abdomen identical with the female, except for the normal sexual differences at the apex of the abdomen. Dorsally, however, there is a sharply marked difference, the tergal plates of the abdomen showing none of the modifications seen in the female, the first segment being not at all produced posteriorly. *Genitalia* (Fig. 7 *D*) consisting of the basal plate, which is continuous with a broad, terminal plate and which bears the small, slender parameres. The preputial sac is marked with small teeth and bears at its inner end a curious structure that is composed in part of a pair of sclerotic rings.

Notes. It is desirable, in connection with this species, to depart somewhat from the programme which I have laid down and to discuss at this point another species which is referable to the genus *Myrsidea*, although it is not my intention to consider the matter of generic limits in general until later.

It will be noted that in *Myrsidea victrix* the first tergite of the abdomen is produced posteriorly in a most curious fashion. That this is the first abdominal tergite and not the metanotum is perfectly clear. The genus *Myrsidea* might be considered as in part defined by this character.

There occurs upon toucans, however, another species of which I have specimens from *Ramphastos swainsonii*, Panama Canal Zone, likewise received through the kindness of Mr Van Tyne. This is apparently the *Colpocephalum extraneum* of Carriker. This agrees with *M. victrix* in all generic characters so closely that the males of the two species are distinguishable only with some difficulty. But in the female *it is the metanotum and not the first abdominal tergite* that is responsible for the curious distortion of the dorsum. The thorax and abdomen of the female of this species are here figured (Fig. 7 *B*).

It is possible that an examination of the many species which at present appear to be referable to *Myrsidea* will bring about a change in my views, but at present I am inclined to regard these two species as fundamentally very closely related and not to be generically separated. Apparently there is some force at work which has brought about a tendency toward a modification

of the portion of the dorsum of the female surrounding the junction of thorax and abdomen, and that force has acted in different ways even in very closely related forms. I am therefore disposed to hold that the matter of whether it is the metanotum or the first abdominal segment that is modified is of no great significance and that forms should not be generically separated on such a basis.

8. **Tetrophthalmus chilensis** Grosse.

Material examined. A male and a female from *Pelecanus thagus*, Lobos de Tierra Island, Peru (R. C. Murphy). As the species was originally described from *Pelecanus* sp. in Chile the identification may be accepted as probably correct.

Female (Fig. 8 *A*). A relatively very large species, of slender form and heavily pigmented, the abdominal tergites appearing as very distinct bands. *Head* with the anterior and lateral margins forming an almost unbroken parabolic curve, the posterior margin deeply concave. Lateral margins with a deep slit (Fig. 8 *H*) in front of the eyes. This slit is backed up by a small, pigmented area. Antennary fossa deep, the ventral side partially covered by a flap. Pharyngeal sclerite and glands lacking. Gular region (Fig. 8 *I*) with a faint plate that bears a few small setae. Mandibles (Fig. 8 *J*) deeply two- or even three-toothed.

Prothorax large, the lateral margins produced into a sharp point and slightly winged; the sternum with a faintly defined plate that bears numerous small setae. *Mesothorax* much reduced, the mesonotum appearing merely as a narrow band; the mesosternum with a very small central plate surrounded by and bearing numerous small setae. *Metathorax* considerably longer than the prothorax, with the sides strongly divergent; the sternum with a well-defined plate that bears numerous small setae. *Legs* of ordinary form, the posterior femora with a series of three combs (Fig. 8 *C*).

Abdomen with the tergal plates strongly sclerotic, each with a single row of small setae along the posterior border, these with the bases in pustulations. Pleural plates distinctly separated from the tergites. Sternites rather faintly defined, that of the third segment with a series of two combs (Fig. 8 *F*) in each posterior lateral angle and that of the fourth segment with a single rather ill-defined comb (Fig. 8 *G*). Sternites of seventh and eighth segments apparently not fused into a single plate, that of the eighth segment with a cluster of small, stout setae at the posterior lateral angles. In the specimen available there are no gonopophyses, as are to be seen in at least one other species of this genus. *Spiracles* extremely large and conspicuous, occurring in the tergites of the third to eighth segments.

Male very similar to the female, but actually somewhat longer, with the abdomen somewhat more sharply pointed, with the middle and posterior legs noticeably larger and stouter, and with the tibiae bearing a thumb-like process at the apex (Fig. 8 *D*). *Genitalia* (Fig. 8 *E*) consisting of an extremely

slender basal plate which extends nearly to the third segment and which connects with an indistinct caudal expansion from which rises the very long, slender and strongly spined preputial sac.

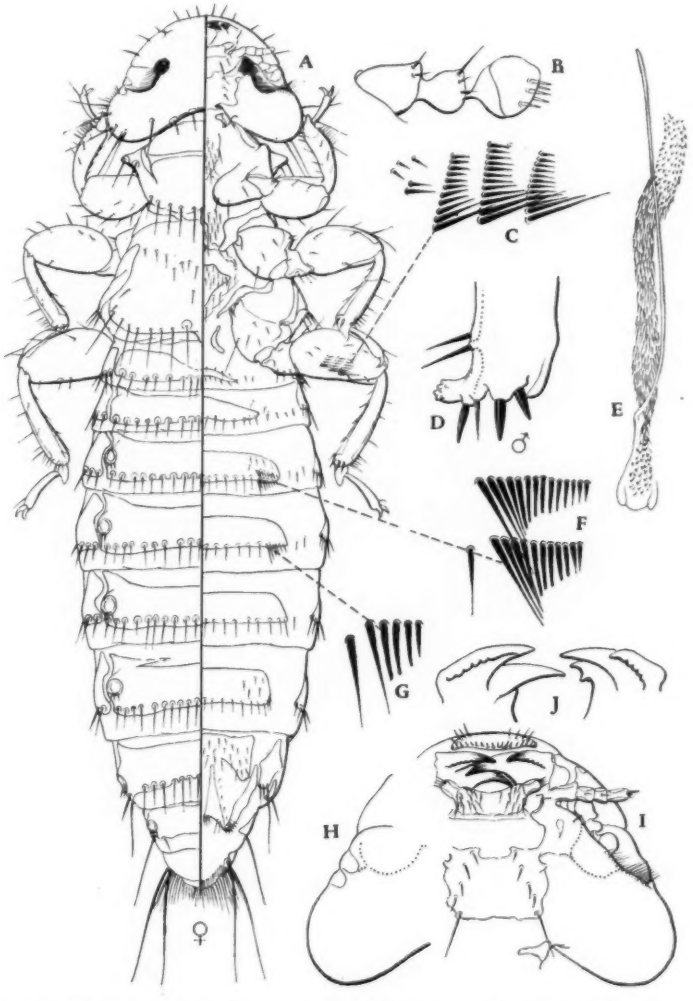

Fig. 8. *Tetrophthalmus chilensis* Grosse. *A*, female; *B*, antenna; *C*, comb of setae from posterior femur; *D*, apex of tibia of male; *E*, genitalia of male; *F*, combs from third sternite; *G*, comb from fourth sternite; *H*, dorsal aspect of lateral margin of head; *I*, portion of ventral aspect of head; *J*, mandibles.

9. **Trinoton anserinum** (Fabricius).

Material examined. A male and a female from *Branta canadensis*, Lake Malheur, Oregon, U.S.A., and a male from *Cygnus bewickii*, Italy. These seem to agree very closely. I am following Harrison, who places *T. conspurcatum* Nitzsch as a synonym of *anserinum*.

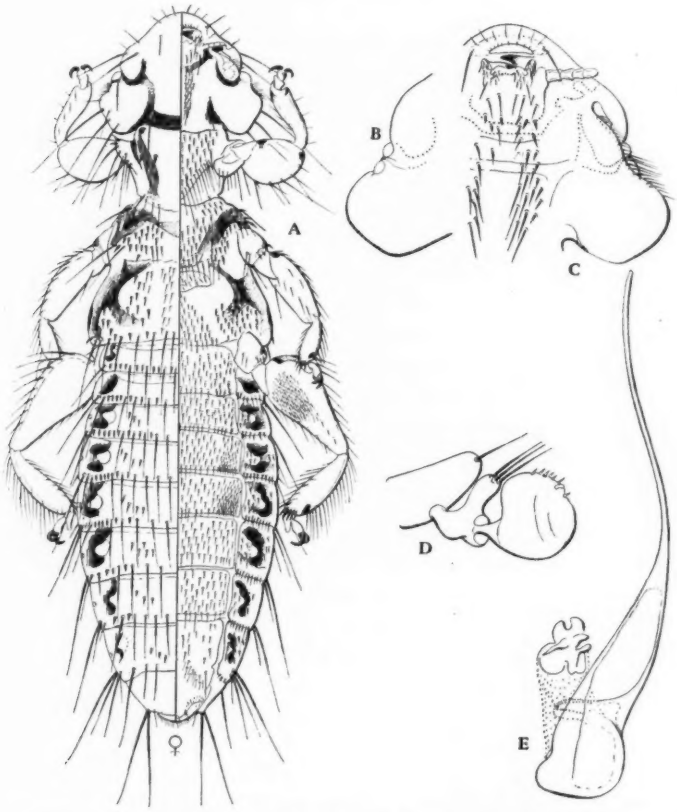

Fig. 9. *Trinoton anserinum* (Fabricius). *A*, female; *B*, dorsal aspect of lateral margin of head; *C*, portion of ventral aspect of head; *D*, antenna; *E*, genitalia of male.

Female (Fig. 9 *A*). A relatively very large form, reaching a length of 8–9 mm., moderately slender and strongly pigmented. *Head* almost triangular, the lateral margins (Fig. 9 *B*) slightly swollen in front of the eyes, but without a notch or a slit. Antennary fossa moderately deep and almost entirely covered beneath, backed up by small areas of pigmentation as shown in Fig. 9 *A*. Antennae (Fig. 9 *D*) apparently but three-segmented and of a rather

peculiar form. Mandibles simple or at the most with two teeth. Gular region without well-defined plate and bearing numerous small setae.

Prothorax large and with sharply angular lateral wings; sternum with numerous small setae. *Mesothorax* unusually large being only slightly narrower and slightly shorter than the metathorax; its ventral side with numerous small setae. *Metathorax* with an ill-defined sternal plate which bears many small setae. Legs peculiar, due to the fact that the coxae are very small and are set at the extreme margin of the body; middle legs noticeably small; tarsi quite short and stout; posterior femora with a sharply defined brush of many small setae on the ventral side.

Abdomen with the tergal and pleural plates apparently continuous, the tergal plates nearly coinciding with their segments in length. Along the sides of the body are conspicuous dark markings, as indicated in Fig. 9 *A*, which are formed by internal sclerotic buttresses that appear to arise from the lateral walls. Spiracles extremely small and inconspicuous, placed at the extreme margin of the abdomen and present on the third to seventh segments of the abdomen. The sternites of the fourth and fifth segments each bear brushes of small, closely set setae.

Male in general very similar to the female. *Genitalia* (Fig. 9 *E*) with an extremely long and slender basal plate which is deeply bifid at its posterior extremity and is continuous with a structure of doubtful homology which bears the preputial sac, the latter beset with small teeth and bearing at its inner extremity a sclerotic structure as indicated in the figure.

(*MS. received for publication* 27. IV. 28.—Ed.)

THE HARVEST BUG.

AN ACCOUNT OF THE PRESENT STATE OF OUR KNOWLEDGE OF THE LARVAL TROMBIDIID MITES ATTACKING MAN.

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(With 2 Text-figures.)

There is still so much confusion with regard to the minute hexapod mites which have for ages plagued man in various parts of the world, and which are known popularly as harvest bugs, harvest mites, bête rouge, rouget, chigger mites, etc., that a review of our present knowledge of the matter may be of use in saving investigators' time in referring to a voluminous and widely scattered literature.

The following list includes the principal harvest mites which are known to attack man. The generic names, which will be discussed presently, are not always those now in use, but were employed when the mites were first recognisably described.

Acarus batatus L., the "batatas" of Surinam.
Leptus autumnalis Shaw, the European harvest mite.
Trombidium americanum Riley, *T. irritans* Riley } N. American harvest mites.
T. tlasahuate Brumpt, the "tlasahuate" or "tlazahuate" of Mexico.
Trombicula akamushi Brumpt, the river fever mite of Japan.
Microtrombidium wichmanni Oudemans, *M. vandersandei* Oudemans, *Trombicula deliensis* Walch, *T. shüffneri* Walch } Dutch East Indies.
Leeuwenhoekia australiensis Hirst, the Australian harvest mite.

In 1758 Linnaeus described the "bête rouge" of Surinam under the name of *Acarus batatus*, and this appears to be the first scientific mention of a harvest mite. The adult form is still unknown.

In 1803–4 Latreille founded the genus *Leptus* to receive a number of hexapod mites which he considered to be mature, and to this genus Shaw in 1790 attributed the English harvest mite which he described under the name of *L. autumnalis*. In 1834 Dugès proved that these mites were only larvae.

It is argued that, since *Leptus* was founded on an Erythraeid and not a Trombidiid larva, Shaw was wrong in his attribution. It is nevertheless

incontestible that much subsequent confusion would have been avoided had the name *Leptus* been retained (or some other name suggested) for all similar larvae until their adults were certainly known.

As regards the other generic names in the above list, *Trombidium* and *Microtrombidium* were conjectural, and have already in some instances proved incorrect, while *Leeuwenhoekia* is founded on larvae of which the adults may well be already known under a different generic name. *Trombicula* alone possesses any validity.

The extra-European forms may first be dealt with, and we turn to Japan, where the occurrence of a disease conveyed by a harvest mite led to a revival of interest in a problem which so many arachnologists had hitherto found baffling. An obscure river fever known as Tsutsugamushi was stated by Tanaka in 1899 to be almost certainly due to a minute mite known locally as Kedani or "hairy mite." This mite—a Trombidiid larva closely resembling our English harvest mite—was named by Brumpt *Microtrombidium akamushi*. It was found plentifully on field mice, especially about the ears, and would readily attack several other mammals—dog, cat, monkey, guinea-pig, etc.—but did not infest insects or spiders.

As usual, great difficulty was experienced in obtaining the complete life-history of the mite, a difficulty due, of course, to the fact that the larvae alone are parasitic and the requirements of the subsequent stages quite unknown.

In 1906 Miyajima obtained nymphs, but it was not till ten years later that Miyajima and Okumara succeeded in rearing adults. Thus in 1916, for the first time, the problem was solved in the case of one species of harvest mite, and these investigators deserve great credit for their success in a field where so many had previously failed.

Their account of the life-history is a little lacking in precision of detail, but it is briefly thus.

The larva remains on the host three or four days, swelling and turning paler, and then drops to earth. In a week or rather more nymphs emerge. They are neither parasitic nor predaceous, but can be reared on mild juicy vegetables—potatoes, melons, etc.—but will not feed on acid fruits such as apples and oranges. Moisture is essential. After growing somewhat they again seek shelter in the earth and "a few days later" assume a form almost like the adult but probably requiring another ecdysis.

"In ten weeks' captivity the nymphs became imagines measuring 0·84–0·98 mm. Only a few of them, however, lived long enough to attain maturity." One of the survivors was a female with a fully developed egg.

It being now possible to recognise the mite in the open, it was sought in infested districts, and large numbers of adults and nymphs were found under fallen leaves or decayed vegetation, in grass, and in the fine sandy mud precipitated by floods. The nymphs and adults appeared to feed largely on the reed *Imperata arundinacea* and the daisy *Artemisia vulgaris*.

The mite is now seen to belong to the genus *Trombicula* Berlese, 1905, and is scientifically known as *Trombicula akamushi*.

The Japanese researches directed attention to similar mites in other oriental regions where diseases of the Tsutsugamushi type occurred—Formosa, the Philippines and the Dutch East Indies—and numerous harvest mites were collected and described.

In 1905 Oudemans described the forms *wichmanni* and *vandersandei*. *Wichmanni* he considers to be the "gonone" of various travellers—Dr Sarasin, Wallace, Martin and others.

Vandersandei is an excellent example of the disadvantage of generic names founded on larvae, for its author has at different times ascribed it to *Thrombidium*, *Allothrombidium*, *Metathrombidium* (all spelt with or without the "h") and finally made it the type of a new larval genus *Shōngastia*.

To these Walch in 1923 added two other forms found on man—*deliensis* and *schüffneri*, and he considers that all four forms—and five others not known to infest man—are in reality *Trombicula*, though at present there is no proof of this.

In 1925 Hirst described an Australian harvest mite under the name of *Leeuwenhoekia australiensis*, assigning it to one of the larval genera of Oudemans.

To turn to the Western Hemisphere, we find four harvest mites of repute infesting man.

The "batatas" of Surinam was the earliest harvest mite to obtain scientific recognition, and as long ago as 1758 Linnaeus named it *Acarus batatus*, but to this day its life-history remains unknown. Another equally famous form is the "tlazahuate" of Mexico. It is mentioned by Lemaire in 1867 without description, but Murray (1877) gives some account of it under the name *Tetranychus tlalsahuate*. Oudemans assigns it to the genus *Microtrombidium*, but apparently it has never been bred out.

The other New World "chigger mites" affecting man were long known as *Leptus autumnalis* and *Leptus irritans* Riley.

Ewing states that *Leptus irritans* has now been reared (? by himself) and that it proves to be the larva of a *Trombicula* already described under the name of *T. cinnabaris*, and he names it therefore *Trombicula irritans*, the specific name *cinnabaris* lapsing.

Thus it would appear that of the extra-European harvest mites known to infest man two only have been successfully bred out, *Trombicula akamushi* in Japan, and *Trombicula irritans* in the United States. With regard to the latter no details appear to have been published. Ewing merely states that the adult has been obtained, but as to how this successful result was brought about we are left entirely in the dark.

We may now turn to the consideration of the European harvest mite—or mites.

The English harvest mite (see Fig. 1) was known as *Leptus autumnalis*

Shaw (1790) until in 1834 Dugès showed it to be a larva. Thenceforward there were various speculations as to the adult genus to which it was attributable. Mégnin (1874) thought it the larva of *Trombidium holosericeum*; Claparède and Andrew Murray (1877) considered it a *Tetranychus*, and the latter gave an account of it under the name *Tetranychus autumnalis* in his *Economic*

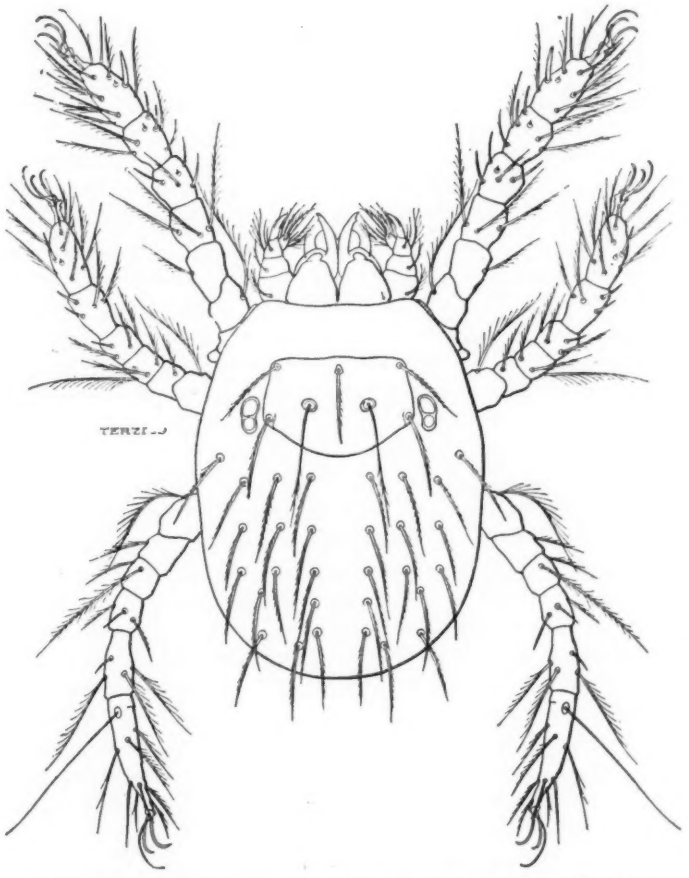

Fig. 1. The Harvest Bug, *Leptus autumnalis* Shaw, greatly enlarged. Reproduced, by permission of Mr Walter Collinge, from the *Journal of Economic Biology*, Vol. x, p. 74.

Entomology. Berlese (1893) attributed it to the mite now known as *Allothrombium fuliginosum*, and Brücker (1897) and Jourdain (1899) agreed. Moniez (1895) thought that several larvae of the genera *Trombidium* and *Rhyncolophus* were concerned.

These attributions were for the most part mere conjecture, though Mégnin

had gone so far as to obtain larvae of *T. holosericeum* which he considered identical with the common harvest mite.

The first serious attempt to breed out the harvest mite seems to be that of Brandis (1897). He proved that the larvae do not bury themselves in the skin but only insert their mouth-parts, but his section of infested skin shows long trumpet-like sucking organs plunged deeply into the tissues. He placed a number of the larvae in sterilised earth, in which they immediately buried themselves, and in a month or six weeks (at the beginning of November) the second or eight-legged stage appeared. It was yellowish, longer and thinner than *Leptus* and suggested *T. holosericeum* by its thick clothing of feathered hairs rendering its abdomen invisible.

That Trombidiid larvae other than the true "*Leptus autumnalis*" would on occasion attack man was proved in 1904 by Heim and Oudemans, who described two other forms, *Thrombidium striaticeps* and *Thrombidium* (*Allothrombidium*, *Metathrombidium*) *poriceps*. These may be considered later.

It was now fairly clear that there was one European harvest mite *par excellence*, though the possibility of the occurrence of other Trombidiid larvae on man was not excluded. The success of the Japanese investigators revived interest in a problem which had remained so long unsolved, and it was now vigorously attacked from three angles. Berlese surveyed the adult Trombidiid fauna; Oudemans described all the larval Trombidiids (and Erythraeids) that could be obtained from any source; and renewed efforts to rear the harvest mite were undertaken by Bruyant in France and by Hirst in England.

In 1912 Berlese published his review of Trombidiid mites—a work of the utmost value. He recognised fifteen genera among which he distributed more than a hundred species. Presumably among these would be found the adult of the harvest mite, or, if as yet unobserved, it would, when discovered, readily find a place in the comprehensive scheme.

In 1913 Oudemans published the second of his remarkable studies of the known larval forms of the Trombidiidae and Erythraeidae. The Trombidiid larvae he distributed among sixteen genera and forty-one species. Most of the genera are founded on larvae, and trouble immediately arises. For example, both Berlese and Oudemans select the generic name *Typhlothrombium* for adult and larva of entirely unrelated forms, and Oudemans has to substitute a new name—*Gahrliepia*. Moreover, as it is inevitable that some of Oudemans' larvae should eventually prove to belong to Berlese's already described adults, their generic names can only be considered as temporary. Some, indeed, have already been changed several times in accordance with changing views as to the adults to which they properly belong.

There is an old story of a Manchester vicar who used to marry couples wholesale at Christmas time and tell them to "sort themselves" as they went out. I suggest that an analogous proceeding would have been entirely proper in the present case. *Leptus* could have been retained with the signification of a Trombidiid larva and the real generic name left for future investigation to

determine. When *Leptus irritans* in America proves to be the larva of *Trombicula cinnabaris* the adjustment is quite simple.

The work of Oudemans is, of course, of the first importance. He has done for the larval forms what Berlese has done for the adults.

Meanwhile, under the stimulus of the Japanese success, renewed attempts were made to breed out the European harvest mite, and in 1910 it was announced with some assurance that the problem had been solved, and that the adult was *Microtrombidium pusillum* Herm. Bruyant had succeeded in obtaining a single nymph from a large number of larvae. Unfortunately it was mounted in a somewhat unsatisfactory condition, and it was not without hesitation that Bruyant and Oudemans decided on attributing it to the above-named adult. Later, Oudemans came to the conclusion that he had been mistaken, but by this time the statement had been widely disseminated and had even found its way into certain text-books.

In 1925 Hirst received from Messrs F. V. Theobald and C. W. Goode some live chickens infested with larvae which on examination proved to be "*Leptus autumnalis*." Several hundreds were placed in jars and cells, but nearly all quickly died—probably on account of insufficient moisture. After thirty-three days a single nymph appeared. It still required another moult to become adult, but being a "nymphal female," possessing copulatory suckers, Hirst considers that it probably chiefly differs from the imago in having two pairs of suckers instead of three. In this case a fairly successful mount was obtained, and the discoverer was able to give an excellent figure of the ventral aspect (see Fig. 2), with details of the cephalothorax, palp and first leg. It has the median constriction characteristic of *Trombicula*, but is rather elongate, with distinctive hairs on the cephalothorax, and Hirst proposes for it the name of *Neotrombicula autumnalis*.

Hirst believes that his nymph is identical with that obtained by Bruyant, though the condition of the latter does not permit of detailed verification. Bruyant had access to some of the preparations left by Brandis, which more or less agreed with his own specimen.

It would appear, then, that three investigators, Brandis, Bruyant and Hirst, have been successful in obtaining nymphs of "*Leptus autumnalis*," though in the case of the last-named only is the specimen in a condition to afford us much information. Clearly the problem is nearly solved, but the astonishing fact remains that the adult of a larva so abundant, so widespread, and so troublesome has apparently never yet been met with in nature. André has quite recently reviewed the adult Trombidiid fauna of France, and to the seven forms previously recorded has added five. Throughout his research he had the harvest mite in view, yet its adult has escaped him, and it cannot be attributed to any one of the twelve species included in the French fauna.

At all events, as was the case in Japan in 1916, we now know the sort of thing to look for. Statements such as those of Picard so lately as 1927—that the adult must be *Allothrombium fuliginosum* because that is the only Trombidiid

found abundantly in a garden infested with harvest mite—are entirely futile. The larva of *A. fuliginosum* is well known and quite distinct, and does not attack man. Nor need we pay much attention to the random statements of

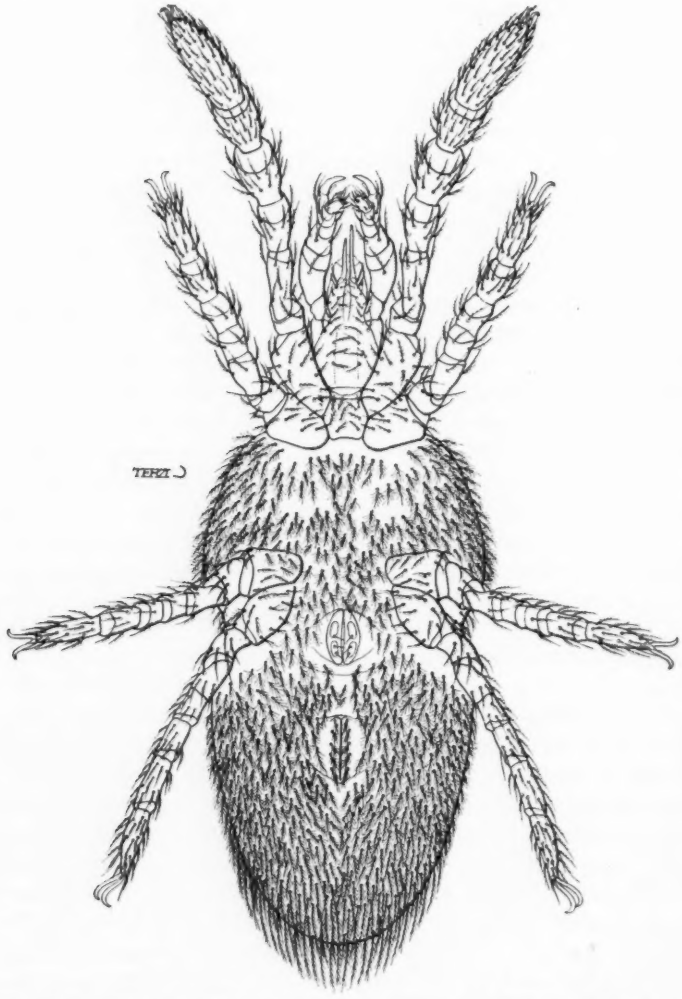

Fig. 2. "Female nymph" of the Harvest Bug, ventral aspect, according to Hirst. Reproduced from the *Annals of Applied Biology*, Vol. XIII, p. 141, by kind permission of the Editors.

various authors as to certain crops—beans, gooseberries, etc.—being especially affected by these mites. As a rule the regions most infested bear no such crops but are open chalk downs. Hitherto we have conceived the object of our

search as a brick-red mite of fair size, more or less like the familiar *A. fuliginosum*. We must change our views, and look for something very small, and not very red. All the harvest mites hitherto reared have proved to be of the *Trombicula* type, and though Ewing has described two gigantic S. American *Trombiculas* 2·5 mm. in length these are quite exceptional, and our quest may be expected to be a yellowish mite, more or less 8-shaped (with a median constriction), and in the neighbourhood of 1 mm. in length. It is probably to be sought in the soil. Hirst thinks the adult has escaped detection so long because it seldom or never appears above ground, and he suggests that specimens might be found in the nests of field mice. The points which still cry out for elucidation are the exact appearance and habitat of the adults and the food—probably vegetable—required by the nymphs.

We saw that in 1904 Heim and Oudemans found two other Trombidiid larvae, one (*striaticeps*) certainly, and the other (*poriceps*) possibly parasitic on man. Their adults are still unknown, but there is a strong probability that *poriceps* is the larva of one of the three or more forms which have been confounded together under the name of *Trombidium* (*Sericothrombium*) *holosericeum*. Bruyant, from two apparently identical adults of *S. holosericeum*, bred two distinct larvae—the *poriceps* and *tectocervix* of Oudemans. A recent opinion of Oudemans (*fide* André) is that there are three very similar mites which have been confused under the name *holosericeum*, (1) the true *S. holosericeum* with *poriceps* for its larva, (2) *T. degeeri* Oud. (= *T. rimosum* Koch and perhaps *T. scarlatinum* Berl.) with *tectocervix* for larva, and (3) *T. latum* Koch (= *T. miliare* Gervais) with unknown larva.

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(*MS. received for publication* 17. IV. 1928.—Ed.)

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The Cambridge University Press has appointed the University of Chicago Press agent for the sale of *Parasitology* in the United States of America and has authorised the following prices: Subscription $10.75 net per volume; single numbers $3.75 net each, double numbers $7.50 net each.

PRINTED IN GREAT BRITAIN BY W. LEWIS, M.A., AT THE CAMBRIDGE UNIVERSITY PRESS